Fall 2015

The Effects of Urbanization on Tick Parasitism Rates in Birds of Southeastern Virginia

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THE EFFECTS OF URBANIZATION ON TICK PARASITISM RATES IN BIRDS OF

SOUTHEASTERN VIRGINIA

by

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B.S. May 2011, Virginia Polytechnic Institute and State University

A Thesis Submitted to the Faculty of
Old Dominion University in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

BIOLOGY

OLD DOMINION UNIVERSITY
December 2015

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ABSTRACT

THE EFFECTS OF URBANIZATION ON TICK PARASITISM RATES IN BIRDS OF SOUTHEASTERN VIRGINIA

Erin L. Heller
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The coastal region of southeastern Virginia is one of the largest urban areas along one of North America's migratory flyways. Because hundreds of avian species use this flyway, understanding factors affecting birds and their health is of paramount concern. Within this region, 14 species of ticks have been documented, all of which may serve as vectors of mammal (including human) pathogens. By sampling birds at sites of varying levels of urbanization within the coastal southeastern urban matrix, I studied the relationship between ticks and their avian hosts, and how this relationship varies seasonally. Mistnets were set-up at five permanent sites and six ad-hoc sites between August 2012 and August 2014 to sample ticks from both migratory and resident birds. During this time, 1886 birds were sampled, and 943 ticks were collected from avian hosts. These ticks were later identified to species in order to determine species-specific avian hosts. Field sites were ranked qualitatively and then quantitatively using national land cover data and ArcGIS in order to determine how urban each site was relative to others; the proportion of birds with ticks was greater at less urbanized (more rural) sites. Percent impervious surface and season played an important role in predicting tick parasitism rates, as did bird life history traits, such as foraging and nesting behavior. The most common life stage and tick species collected from birds were larval rabbit

ticks (*Haemaphysalis leporispalustris*), followed by larval bird ticks (*Ixodes brunneus*). This study demonstrates how levels of urbanization can influence tick parasitism rates on birds and increases knowledge of the corresponding relationship between urbanization and disease prevalence, which ultimately could affect human health risks.

My thesis is dedicated to my grandmother, Margaret “Grams” Kaiser. She instilled in me my love for nature and more specifically my fascination with birds. Her wonder for the world around her and her compassion for its creatures are traits that I will carry with me for the rest of my life.

ACKNOWLEDGMENTS

I would like to extend my gratitude and appreciation to my advisor, Dr. Eric L. Walters, for encouraging me to pursue my interests in avian ecology and for working with me to learn about the world of tick biology. Learning to band birds with the utmost care for their health and safety is a skill I will take with me throughout my life, both in academia and out, and I am very thankful for everything he has taught me during the past three years.

I also would like to express my sincere appreciation for his thorough efforts in the editing and revision processes of my thesis. Additional thanks are extended to my committee members, Dr. Holly D. Gaff and Dr. R. Jory Brinkerhoff, for all of their time and advice. Dr. Gaff has spent countless hours in the field with me and in the lab looking at ticks under microscopes. Without her assistance, I surely would not be where I am today, and Dr. Brinkerhoff has provided his expertise in bird-tick interactions.

I would like to thank Weyanoke Wildlife Sanctuary, Paradise Creek Nature Park, Hoffler Creek Wildlife Preserve, The Nature Conservancy, and the Virginia Zoo for allowing me to conduct research on their properties. In particular Randi Strutton, Helen Kuhns, Joe Rieger, David Koubsky, Mike Shoen, Linda Cameron, and Roger Sweeney were all instrumental in providing me access to various sites. I also thank Dr. Hynes and Dr. Gauthier and all of the graduate students and field assistants in the Walters lab, the Gaff lab, and the Hynes lab who helped make this project possible, specifically Natasha Hagemeyer, Lindsey Bidder, Robyn Nadolny, Pam Kelman, Chelsea Wright, Dorothy Paine, Alexis White, Annie Sabo, Ally Lahey, Amy

Johnson, Tyler Chavers, Noel Brightwell, Jessica Vincent, Paul Dawson, Jessica Asfari, Cathy Roberts, David Swisher, Michael Bailey, Sean Millman, Terisha Dunn, Tomeka Bandy, Elena Flicken, Maggie McDonald, Michael Goddard, Adrienne Ashby, and any others I may be missing. More specifically, Natasha trained me to mistnet and band birds safely; Lindsey was invaluable in assisting me with my GIS work; Robyn spent many early mornings with me fighting off mosquitoes and horse flies while waiting for birds to fly into the nets; Chelsea ran all of the PCR analyses; and everyone else assisted with field work or data entry.

Daniel Vanselow and Benjamin Augustine assisted me in an R crash-course and were immensely helpful. Additional thanks are extended to George McLeod for assisting me further with GIS work. Old Dominion University's Research for Undergraduates in Math and Sciences program (RUMS) provided undergraduate assistance throughout my field work as well. Mike Aherron from the Department of Forestry, David Cutherell from ODU, Sarah Sumoski from Paradise Creek Nature Park, and The Virginia Aquatic Resources Trust Fund through The Nature Conservancy and Barney Environmental provided me with invaluable information on the vegetation at various sites. Finally, a huge thanks goes to the agencies that helped fund my study, including: Old Dominion University, the Virginia Academy of Science, the Virginia Society of Ornithology, and ODU’s Alumni Association.

I would like to thank my father, mother, and brother who all have been incredibly supportive of my endeavors in graduate school. They have provided me with unconditional love and patience throughout my graduate school adventure and helped keep me sane when the going got tough. A huge thanks goes to Olivia Soska.

Her support and unwavering desire to assist me in any way possible are unmatched and greatly appreciated. Additional thanks are extended to the wonderful friends I have made in Norfolk, especially my graduate student family at ODU, and to all of my friends from all other walks of life.

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CHAPTER I

INTRODUCTION

Ticks are ectoparasites that rely on parasitizing hosts to get the nutrients they need to survive (Nelson et al. 1975, Chanie et al. 2010). Ectoparasites include, but are not limited to, ticks, mites, lice, mosquitoes, and fleas (Chanie et al. 2010, Smith and Titchener 2011), all of which attach to their hosts' outer epidermis and insert a feeding tube into the skin in order to consume blood (Endo 1978). Different types of ectoparasites have varying host preferences, and different tick species, the ectoparasites focused on for this study, follow this pattern (Cumming 1998, Christe et al. 2007). Many tick species are commonly found on mammals, such as white-tailed deer (*Odocoileus virginianus*) and white-footed mice (*Peromyscus leucopus*; Anderson et al. 1983, Magnarelli et al. 1995), whereas other ticks parasitize birds, reptiles, and amphibians (Sonenshine and Stout 1970, Anderson et al. 1986, Nicholls and Callister 1996, Poupon et al. 2006).

Because ticks are able to transmit numerous pathogens that can affect human health, such as Lyme disease and tularemia, understanding the environmental factors that can influence the relationship between ticks and their hosts is imperative (Belman 1999, Kjemptrup and Conrad 2000, Ringdahl 2001). For example, seasonality, temperature, precipitation, humidity, and resource availability all can affect the relationship between parasites and their hosts (Guerra et al. 2002, Altizer et al. 2006). Ticks can survive long periods of time between blood meals, and therefore can survive long periods of time without access to the water they extract from their hosts' blood (Saeuer et al. 1995, Anderson and Magnarelli 2008); because of this, ticks rely heavily on their environment to remain moist in order to prevent death by desiccation (Wilkinson and Wilson 1959, Guerra et al. 2002, Yoder et al. 2008). Ticks often require high humidity in their environments and adequate moisture in the leaf litter and vegetation on the ground, where they live, in order to survive (Lees 1946, Heath 1979, Needham and Teel 1991, Stafford 1994, Schulze et al. 1995, Randolph and Storey 1999, Guerra et al. 2002, Herrman and Gern 2012). Teasing apart the nuances of these relationships can assist one in comprehending how tick hosts are affected by various disease pathogens and in turn what risks these pathogens pose to humans.

TICK LIFE HISTORY

There are over 840 species of ticks in the world (Anderson 2002), yet only 14 have been documented in coastal southeastern Virginia (Sonenshine 1979). These ticks include: *Dermacentor albipictus* (winter tick), *Dermacentor variablis* (dog tick), *Amblyomma maculatum* (Gulf Coast tick), *Amblyomma americanum* (lone star tick), *Ixodes scapularis* (blacklegged tick), *Ixodes affinis* (no common name), *Ixodes brunneus* (bird tick), *Ixodes dentatus* (no common name), *Ixodes cookei* (woodchuck tick), *Ixodes texanus* (raccoon tick), *Ixodes marxi* (squirrel tick), *Haemaphysalis leporispalustris* (rabbit tick), *Rhipicelphalus sanguineus* (brown dog tick), and *Carios Ornithodoros kelleyi* (bat tick; Table 1). Ticks are bloodsucking arachnid ectoparasites that are categorized into three major families: Argasidae (soft-bodied ticks), Ixodidae (hard-bodied ticks), and Nuttalliellidae (only found in Africa),

Table 1. The 14 species of tick found in coastal southeastern Virginia (Sonenshine 1979).

Scientific Name	Common Name
Dermacentor albipictus	winter tick
Dermacentor variablis	dog tick
Amblyomma maculatum	Gulf Coast tick
Amblyomma americanum	lone star tick
Ixodes scapularis	blacklegged tick
Ixodes affinis	none
Ixodes brunneus	bird tick
Ixodes dentatus	none
Ixodes cookei	woodchuck tick
Ixodes texanus	raccoon tick
Ixodes marxi	squirrel tick
Haemaphysalis leporispalustris	rabbit tick
Rhipicelphalus sanguineus	brown dog tick
Carios Ornithodoros kelleyi	bat tick

though primarily hard-bodied ticks are known to be found in the study region of southeastern coastal Virginia (Anderson 2002, Nadolny et al. 2011, Wright et al. 2011). The only soft-bodied tick reported in Virginia is *C. kelleyi* (bat tick, Sonenshine 1970).

The majority of Ixodid ticks have four life stages: egg, larva, nymph, and adult (Gardiner and Gettinby 1981, Spach et al. 1993). Larval ticks are easily identifiable from nymphal and adult ticks, as larvae have six legs, whereas nymphs and adults have eight (Anderson and Magnarelli 2008). However, morphological identification to species is very difficult while ticks are in their larval and nymphal stages (Clifford and Anastos 1960). Once ticks molt into their adult life stage, they generally can reliably be sexed and identified to species morphometrically (Ginsberg et al. 2004).

In order for ticks to molt into their next life-stage, they must have a blood meal, which they are able to find through detecting shadows, heat, odor, vibrations, and kairomones using their Haller's organ, a sensory organ located on the first pair of legs (Klompen and Oliver 1993, Durland 1995, Sbarbati and Osculati 2006, Süss et al. 2008). Larvae and nymphs will parasitize smaller hosts, including but not limited to rodents, birds, and various reptiles and amphibians, in addition to the larger hosts that adult ticks prefer (Randolph and Storey 1999, Wilson et al. 1985). Once a suitable blood meal has been obtained, ticks feed to repletion, enter diapause which can last for 8 months (Obenchain and Galun 1982, Steele and Randolph 1985, Randolph 1997), and subsequently molt into their next life stage (larvae molt into nymphs, and nymphs molt into adults) or mate as adults and then die (Sonenshine 2006). Adult females, in general, are larger than adult males, as females require larger blood meals to support egg production (Daniels et al. 1989, Sonenshine 1991, Sonenshine 2006, Anderson and Magnarelli 2008). Most adult females mate, feed to repletion, and then lay clusters of thousands of eggs, though females of some species will feed to repletion before mating. Some species of tick, such as *A. americanum*, will mate multiple times before dying (Spielman et al. 1985, Sonenshine 1991, Sonenshine 2006). Adult males typically do not feed to repletion but instead begin feeding and are often distracted by female sex hormones, causing the males to search for females to mate with, though this behavior is also variable depending upon tick species. Following mating, which occurs either once or multiple times depending upon species, both female and male ticks die (Andrews and Bull 1980, Andrews 1982, Kiszewski et al. 2001).

TICK FEEDING HABITS

Some species of tick show preference for certain hosts, while others are more indiscriminate in their feeding habits and are known to parasitize a suite of hosts, ranging from reptiles and birds to small mammals and humans (Tugwell and Lancaster 1962, Anderson 1989, Black and Piesman 1994, Ostfeld and Keesing 2000, Jongejan and Uilenberg 2004). Host preference also varies depending upon tick life stage (Wilson et al. 1985, Randolph and Storey 1999). For example, large mammals often have higher burdens of adult ticks, whereas birds and reptiles are more likely to serve as hosts to ticks in all life stages (Wilson et al. 1985, Levine et al. 1997, Randolph and Storey 1999, Eisen et al. 2004).

Although mammals serve as the primary hosts for the majority of tick species along the east coast of the United States, birds are also important hosts (Giardina et al. 2000). Because birds tend to have larger home ranges and migratory movements than mammals, birds also increase the potential for novel tick species and disease pathogens to spread over landscapes (Weisbrod and Johnson 1989, Scott et al. 2001, Peters 2009). Therefore, the relationship between birds and ticks across varying habitat types and areas is an important area of investigation.

Tick host selection can be separated into distinct phases (Lees 1948, Camin 1963, Camin and Drenner 1978): (1) finding a host and (2) distinguishing among hosts. Because ticks are not able to jump or fly, they therefore use outstretched front legs to climb onto hosts as they brush by (Camin and Drenner 1978); hosts, therefore, must be in close proximity to the ground in order for ticks to successfully parasitize them. To find hosts, ticks either ambush or actively pursue their prey. Ticks that ambush, such as the blacklegged tick (*I. scapularis*) and the American dog tick (*D. variablis*), climb vegetation and wait for a passing host (Sonenshine 1991). Other species such as the lone star tick (*A. americanum*) actively pursue their hosts (a strategy akin to hunting; Sonenshine 1985). Because ticks spend their lives on or near the ground, potential hosts, including birds, that do not nest or forage on the ground are not commonly parasitized by ticks (Semtner and Hair 1973a,b, Schulze et al. 1995).

Once they find their host, ticks insert a feeding tube, called the hypostome, into their hosts' skin (Keirans and Litwak 1989, Anderson 2002, Jongejan and Uilenberg 2004). Many species of tick secrete a saliva that "cements" them to their hosts and has anesthetic properties, an adaptation that enables these ticks to feed undetected (Bowman et al. 2008, Francischetti 2009, Wolańska-Klimkiewicz et al. 2010). Hard-bodied ticks ingest large amounts of blood relative to their size (Brown and Knapp 1980, Obenchain and Galun 1982). To do this, they filter out the proteins in the blood and return both water and electrolytes back into their hosts (Munderloh and Kurtti 1980, Anderson 2002). Hard-bodied ticks feed for several days and up to two weeks until fully engorged, whereas soft-bodied ticks finish feeding within a few hours of attachment, as they do not filter blood as they ingest it (Lawrie et al. 1999, Anderson 2002, Anderson and Magnarelli 2008).

Because hard-bodied ticks return water and electrolytes in their hosts, ticks are able to spread pathogens (Araman and Said 1972, Munderloh and Kurtti 1980, Anderson 2002). If a host is a reservoir for a particular pathogen, the tick may obtain the pathogen while feeding and then be able to transmit the pathogen to a previously uninfected host upon its next feeding (Gauthier-Clerc et al. 1998, Piesman and Sinsky 1988). This relationship is highly complex, as reservoir competence among not only different taxonomic groups but also among species within the same taxonomic group is variable. Therefore, some hosts are more likely to transfer a given pathogen to a previously uninfected tick than other hosts (Richter et al. 2000, Ginsberg et al. 2005). Understanding these relationships is further complicated in that there is little known about avian host competence for most tick-borne pathogens (Bjoersdorff et al. 2001).

TICK-BORNE DISEASES

Next to mosquitoes, ticks are the second most common agent of vector-borne diseases in the world but rank first as the most common agent of human vector-borne diseases affecting wild and domestic animals (Doan-Wiggins 1999, de la

Fuente et al. 2008). Ticks are also the most common agent of vector-borne disease in North America (Spach et al. 1993).

Different tick species may serve as vectors of pathogens such as *Borrelia burgdorferi*, *Babesia* spp., *Ehrlichia chaffeensis*, *Anaplasma phagocytophilum*, *tularemia*, *Rickettsia rickettsii*, and *Rickettsia parkeri* (Burgdorfer 1975, Johnson et al. 1984, Markowitz et al. 1985, Anderson et al. 1993, Golightly and Benach 1999, Stuen 2007, Wright et al. 2011). A few of these diseases will be discussed briefly but without great detail. The disease component to this study was limited and primarily focused on why understanding relationships between birds and ticks are of global importance.

Lyme disease is the most common tick-borne disease in the United States (Fraser et al. 1997). Larval ticks are not infected until they ingest the pathogen's spirochetes from an infected host reservoir (Matuschka 1992). The infected larvae keep the spirochetes through their molt to the nymphal stage and are able to transmit *Borrelia burgdorferi* to future hosts (Gatewood et al. 2009). This is important because birds parasitized by infected ticks have the potential to disperse the pathogen outside of the areas where the pathogen currently is found, causing the pathogen to further affect human health (Scott et al. 2001, Ogden et al. 2008, Scott et al. 2010). Because *B. burgdorferi* is not known to be transmitted transovarially from an infected adult female to her eggs (Patrican 1997). This suggests that ticks that test positive for *Borrelia burgdorferi* ingested the pathogen from an infected host (Donague et al. 1987).

Tularemia, commonly carried by *H. leporispalustris*, is caused by the bacterium *Francisella tularensis* which attacks white-blood cells. It is considered highly infectious, though there are numerous subspecies of this bacterium that vary in their virulence (Sjostedt et al. 1997). Babesiosis is caused by parasites in the genus *Babesia* that attack the red blood cells of their hosts (Saini and Sankhala 2015). The most common *babesia* species that affects humans is *Babesia microti* (Homer et al. 2000). The parasites that cause the different strains of babesiosis are often called piroplasms due to their shape and are capable of infecting numerous vertebrate hosts (Ranjbar-Bahadori et al. 2012). Anaplasmosis, a group of bacterial tick-borne diseases, is another common tick-borne disease found in North America (Lin et al. 2007). The two most common strains are human granulocytic ehrlichiosis, caused by *Anaplasma phagocytophilum*, and human monocytic ehrlichiosis, caused by *Ehrlichia chaffeensis* (Adachi et al. 1997). Newly recognized to North America is Tidewater spotted fever, caused by *Rickettsia parkeri*, a close relative to the more commonly known Rocky Mountain spotted fever, a life-threatening tick-borne disease for humans caused by *Rickettsia rickettsii* (Burgdorfer 1975, Dantas-Torres 2007).

TICKS AND URBANIZATION

Urbanization is defined as the alteration of natural habitats into anthropogenic communities (Hamer and McDonnell 2009). The effects of urbanization are increasingly relevant in today's world and have substantial ecological consequences as habitats are destroyed or simplified (Peressin and Cetra 2014, Alberti 2015, Aronson et al. 2015). More specifically, it is estimated that the quantity of developed land within the United States grew on average 1.6% per year between the 1970s and early 2000s (Theobald 2005). This increase in urbanization causes the displacement of wildlife as suitable habitat is lost and is therefore considered a key driver of biodiversity loss (Sol 2014, Alberti 2015, Riem 2015). Many species either disappear from their former habitats all together or are restricted to fragmented land within urban settings (Bradley and Altizer 2006), causing species diversity and richness for most animals, including birds, to decrease (Philippe et al. 2002, Melles et al. 2003, Shochat et al. 2006).

As numerous animal species are excluded from natural habitats, so too are the ectoparasites associated with such wildlife (Le Gros et al. 2011, Calegaro-Marques and Amato 2014, Webster et al. 2014). Therefore, addressing how urbanization affects the biodiversity of potential tick hosts is imperative to the comprehension of tick and tick-borne disease spread. In this study, the relationship between avian hosts and their tick ectoparasites was examined along an urbanization gradient. In theory, as host diversity and richness decreases, the expectation is that tick diversity and abundance should follow suit (Le Gros et al. 2011, Calegaro-Marques and Amato 2014). The obvious mechanism for such a pattern would be that ectoparasites are more likely to die from lack of obtaining a blood meal necessary for their survival (Nelson et al. 1975, Chanie et al. 2010). Additionally, because ticks rely heavily on humidity and moisture in their environment in order to prevent desiccation, the lack of vegetation and leaf litter required to maintain moisture in urban areas further prohibits tick presence (Naithani and Bhatt 2012, Alberti 2015, Shimadera et al. 2015).

TICK-BIRD INTERACTIONS

Birds serve as hosts for many species of hard-bodied Ixodid ticks (Scott et al. 2012). Because birds fly, they could serve as an important dispersal agent of ticks, in contrast to the shorter distance dispersal provided by mammalian, reptilian, and amphibian hosts (Smith et al. 1996, Scott et al. 2001, Ogden et al. 2008). Birds that fly are unique in their mobility and therefore exhibit potential to spread diseases in a short period of time (Anderson and Magnarelli 1984, Scott et al. 2001), facilitating rapid transport of pathogens to novel areas (Reisen 2001, Hamer et al. 2012a). This is primarily a concern for migratory bird species, since they often travel great distances very quickly during their migrations, although non-migratory species also can move long distances rapidly (Ahola et al. 2007); therefore, understanding the relationship between ticks and both resident and migratory species is paramount to the comprehension of tick-borne pathogen spread and the implications pathogen spreading has on public health.

Given the phenology of the tick life cycle, combined with the mobility and migratory tendencies among birds, seasonality is also likely to play a role in bird-tick relationships (Altizer et al. 2006). For example, the majority of *I. scapularis* larval ticks are most common in the environment from July to September, which coincides with the fall migration of migratory bird species in North America (Wilson and Spielman 1985, Battaly et al. 1987). However, very little is known about the seasonality of tick species during different life stages in southeastern Virginia.

STUDY GOALS

This study was conducted at 5 permanent and 6 ad-hoc field sites along an urbanization gradient in the coastal region of southeastern Virginia along a major migratory flyway from August 2012 to August 2014. Birds were caught year-round using mistnets at each field site, and ticks found on birds were removed and later processed in the lab. In Chapter II, I test the effect of urbanization on the likelihood of ticks parasitizing birds and use models that determine the best predictors of tick parasitism on birds. In Chapter III, I look at how both bird and tick phenologies affect the likelihood of an individual host being parasitized and theorize on why these associations exist. Chapter IV provides a summary of the findings and puts these findings into the context of previous work on the subject. This study is the first, to my knowledge, to examine the relationship among urbanization, birds, ticks, and tick-borne pathogens year-round.

CHAPTER II

THE EFFECT OF URBANIZATION ON THE RELATIONSHIP BETWEEN TICKS AND THEIR AVIAN HOSTS

INTRODUCTION

Urbanization can be roughly defined as the alteration of natural habitats into anthropogenic communities (Hamer and McDonnell 2009). The effects of urbanization are increasingly relevant in today's world (De Silva and Marshall 2012). Between 1970 and 2000, it was estimated that the quantity of developed land within the United States grew on average 1.6% per year (Theobald 2005), and within the next 20 years, it is anticipated that at least two-thirds of the human population will live in cities (Bradley and Altizer 2006). This increase in urbanization and consequent movement of human populations cause the displacement of wildlife as suitable habitat is lost (Bradley and Altizer 2006, Hunt et al. 2013, Schaefer and Gonzales 2013), causing many species to either disappear from cities all together or be restricted to fragmented land within urban settings (Bradley and Altizer 2006). This, in turn, often reduces both species diversity and richness for most animals, including highly mobile animals, such as birds (Philippe et al. 2002, Melles et al. 2003). Most animals are not as mobile as birds given their physiological restraints to movement (Padian and Chiappe 1998); however, despite the ability of birds to rapidly travel great distances, most birds will not simply leave areas that previously provided them with the resources needed to survive (Haas 1998). Therefore, many local populations become extinct in highly-urbanized areas, causing species diversity to decrease as habitat is lost (Shochat et al. 2006).

URBANIZATION AND WILDLIFE

Habitat alteration, often referred to as habitat degradation, associated with increased urbanization negatively affects most wildlife (Theobald et al. 1997). The study of habitat change caused by urbanization therefore is well studied, particularly as it negatively affects species richness due to habitat fragmentation and reduction in resources (McKinney 2008, Nagendra et al. 2013, Aronson et al. 2014). These negative effects are often amplified because of the disproportionate abundance of invasive, or non-native, species in urban settings (Aronson et al. 2015, Veran et al. 2015). Invasive species are known for out-competing native species for resources and often are able to survive in areas where native species cannot due to the generalist requirements of most invasive species (Yan et al. 2001, Allendorf and Lundquist 2003, Crooks et al. 2004, Joseph et al. 2014); therefore, invasive species are more common in urban areas because they are adapted to survive in the altered conditions urbanization provides (Crooks et al. 2004, Joseph et al. 2014).

One of the less obvious effects of increased urbanization is the loss of the public's appreciation for and understanding of nature, which in turn sends negative messages to children that playing outside in nature is unpleasant (Theobald et al. 1997, Patterson et al. 2003, Sandry 2013). This phenomenon is often referred to as the nature deficit disorder (Sandry 2013). As members of society become more removed from wildlife due to the expansion of developed land, they tend to lose an understanding of the importance of preserving natural habitats and the flora and fauna it supports (Turner et al. 2004). This, in term, affects legislature and decision-making processes concerning the environment (Messmer 2000). As people either care less or understand less about wildlife, potentially damaging laws could be put in place and protection of natural resources will likely be compromised (Patterson et al. 2003). One way to minimize these negative effects of urbanization is to cluster developments in order to reduce urban sprawl and to better educate the public on the implications of increased development on wildlife (Theobald et al. 1997, Marvier et al. 2004).

Another overlooked area concerns the relationship between urbanization and wildlife and the effect increasing urbanization has on disease pathogen transmission rates. While urbanization generally reduces the abundance of parasites, transmission of disease pathogens may increase with increased levels of urbanization (Bradley and Altizer 2006). Changes in the environment often affect the life histories of vectors, disease pathogens, and hosts (Patz et al. 2000, Daszak et al. 2001). While urbanization typically decreases the prevalence of parasites in general, the effects that urbanization have on pathogen prevalence is less understood (Bradley and Altizer 2006). Often, as communities and ecosystems are fragmented, species richness decreases (Melles et al. 2003). This introduces the question of whether a decrease in biodiversity due to urbanization may increase the proportional abundance of reservoir-competent hosts for pathogens. The dilution effect suggests that reduced species richness, as a result of habitat destruction, could increase the proportional abundance of competent hosts (Schmidt and Ostfeld 2000, Bradley and Altizer 2006, Swaddle and Carlos 2008, Pongsiri et al. 2009). Not every organism is a competent reservoir for a given pathogen, however, and whether particular avian taxa are competent or not is a relatively under-studied topic, as most studies looking at the dilution effect have focused on highly competent mammalian reservoirs such as white-footed mice (Nupp and Swihart 1996, LoGiudice et al. 2003). Because habitat destruction and biodiversity loss have been associated with an increase in pathogenic diseases (Pongsiri et al. 2009), habitat destruction may also increase pathogen hotspots along animal migration routes, including avian migratory flyways, as suitable stop-over sites are lost (Altizer et al. 2011).

Despite the negative effects urbanization has on many environmental systems, the quantity of both birds and mammals in developing or highly urbanized areas has increased over the past several generations, as various species adapt to changing environments, invasive species move-in, and habitat restoration projects are implemented (Savard et al. 2000, Luniak 2004). The influx of wildlife inhabiting areas in and around cities, a phenomenon sometimes termed synurbanization, is an emerging field of study. The term relates how organisms adapt or adjust to urban conditions (Babinska-Werka et al. 1979, Luniak 2004) but is only applicable for animals that “choose” to enter urban areas, rather than animals that migrate through or are intentionally brought in by humans (Luniak 2004).

URBANIZATION AND ECTOPARASITES

Because of the displacement of wildlife due to urbanization, it follows that ectoparasites, such as ticks, associated with such wildlife likely are affected by urbanization as well. Ticks require specific microclimates, including high humidity and adequate leaf litter, combined with access to vertebrate hosts (Schulze et al. 1995). These conditions are readily available in rural areas but often are not as easily met in urban areas (Hoch et al. 1971, Semtner et al. 1971). Forested areas with high edge-cover, for example, typically provide better habitat for many species of ticks than manicured yards or open fields (Maupin et al. 1991, Ostfeld et al. 1995, Peters 2009). Areas comprising fragmented wooded lots with a variety of understory also support high numbers of ticks and their vertebrate hosts (Glass et al. 1994, Brownstein et al. 2005).

Habitat fragmentation and an increase in urbanization have resulted in a decline in forested areas across the United States and a decline in animal species diversity (Maset et al. 2000, Melles et al. 2003). Since birds, along with mammals, amphibians, and reptiles, typically are negatively affected by urbanization, understanding how tick prevalence varies across urban to rural landscapes can provide valuable information on bird-tick relationships (Blair 1996; Fokidis et al. 2008, McKinney 2008). Additionally, understanding mechanisms behind the relationship between ticks and the likelihood of them encountering both bird and human hosts is imperative to the field of public health (Kowalczyk and Smith 2008, Hamer et al. 2012b).

HYPOTHESES

For this study, I addressed three hypotheses:

(1) Impervious Surface Hypothesis: Percent impervious surface is negatively related to tick parasitism rates on birds as areas with more impervious surfaces tend to be more urban (Arnold and Gibbons 1996, Morse et al. 2003). Because ticks cannot survive for extended periods of times in areas with high impervious and impermeable surface, birds that live in or near areas that have high impervious and impermeable surface cover (such as highly urban areas) are unlikely to be parasitized by ticks.

(2) Environmental Constraint Hypothesis: Birds in more urbanized areas exhibit lower tick burden than less urbanized areas (Arnold and Gibbons 1996, Morse et al. 2003, Bradley and Altizer 2006). The lack of suitable tick habitat because of higher cover of impervious surfaces and, in turn, lack of suitable vertebrate hosts, in urban areas limits the number of ticks that can survive, reducing potential tick burdens (Bradley and Altizer 2006). I predicted that proportional change in tick presence with increasing urbanization will vary among avian species and that all avian hosts in more urbanized areas will exhibit less tick burden than avian hosts in less urbanized areas.

(3) Host Constraint Hypothesis: Ticks exhibit lower host specificity in more urbanized areas. Because there are fewer species of birds in more urbanized areas (Clergeau et al. 1998), this lack of diversity constrains the ability of ticks to show host preference; thus, non-preferred hosts (ie hosts not typically parasitized in rural areas) should exhibit greater tick burden, and therefore be more likely to vector pathogens, in more urbanized areas.

METHODS

PERMITS

In order to conduct this study, several federal and state permits and the International Animal Care and Use Committee (IACUC) approvals were required. These research compliances include: Old Dominion University IACUC Protocol # 12-006, Old Dominion University IACUC Protocol # 13-018, The Nature Conservancy

Permit for Stephens Tract in Chesapeake, Virginia, US Department of the Interior Federal Bird Banding Permit #23803, Virginia Department of Game and Inland Fisheries Wildlife Salvage Permit # 044737, Virginia Department of Game and Inland Fisheries Scientific Collection Permit #044735, Commonwealth of Virginia Department of Conservation and Recreation Research and Collecting Permit #FLKPYR...-RCP-030512, the Federal Fish and Wildlife Permit #MG71673A-0, and the Department of Conservation and Recreation Division of Natural Heritage Natural Area Preserve Research and Collecting Permit # DNH-MTR01-12.

SITES

This study took place at eleven sites (5 permanent and 6 ad-hoc) varying in size from 0.8 ha to 410.5 ha in the coastal southeastern region of Virginia. Each site was chosen from a larger list of sites used as part of other tick-related studies at Old Dominion University and represented a particular level of urbanization along an urbanization gradient. Permanent sites included: Weyanoke Bird and Wildlife Sanctuary (3.2 ha), Paradise Creek Nature Park (16.2 ha), Hoffler Creek Wildlife Preserve (57.5 ha), Jacobson Tract (21.0 ha), and Stephens Tract (Chesapeake, 148.1 ha; Fig. 1; Table 1). Hereafter, these sites will be referred to as Weyanoke, Paradise, Hoffler, Jacobson, and Stephens, respectively.

Ad-hoc sites included: Hidden Cove (0.8 ha), Virginia Zoo (21.0 ha), Kiptopeke State Park (216.9 ha), Suffolk Landfill (152.0 ha), York Site (410.5 ha), and Blackwater Ecological Preserve (128.7 ha; Fig. 1; Table 1). Hereafter, these sites will be referred to as Hidden Cove, Virginia Zoo, Kiptopeke, Suffolk, York, and Blackwater respectively.

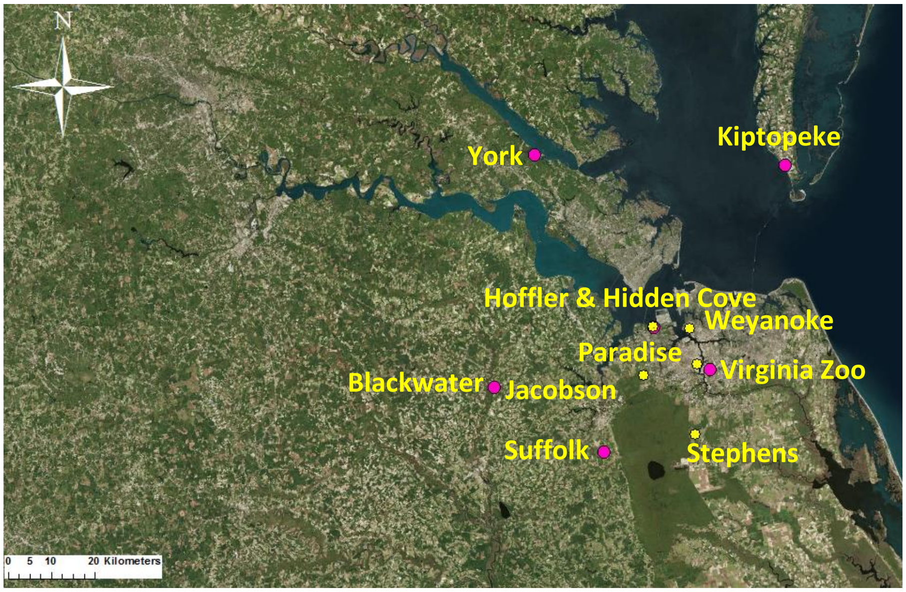

Figure 1. Permanent (yellow) and ad-hoc (purple) field sites in coastal southeastern Virginia.

On average, permanent sites were sampled every other week from August 2012 to August 2014, and ad-hoc sites were sampled haphazardly as time allowed. More specifically, Hoffler and Stephens were both sampled from August 2012 to 2014. Weyanoke and Paradise were sampled from November 2012 to August 2014, and Jacobson was sampled from June 2013 to August 2014.

PERMANENT SITE DESCRIPTIONS

WEYANOKE

Weyanoke Bird and Wildlife Sanctuary is a small preserve located in the heart of Norfolk, Virginia, that was created in 1979. Based on estimates provided by those who run the preserve and on my visual estimates, the sanctuary is about 50% forest, 20% flower beds, 25% open green space, and 5% stream. It consists of a mixed hardwood-conifer forest, with the dominant species being loblolly pine (*Pinus taeda*), white oak (*Quercus alba*), and flowering dogwood (*Cornus florida*). Understory species consist primarily of several fern (*Asplenium spp.*) species, English ivy (*Hedera helix*), and numerous species of flowering annuals and perennials. The preserve is heavily managed, and the vegetation is regularly pruned and trimmed.

PARADISE

Paradise Creek Nature Park is a 2.5 year old urban park in Portsmouth, Virginia, run by the Elizabeth River Project. The make-up of the park as estimated by park officials and agreed-upon by myself is about 40% wooded, 30% wetland, 25% meadow, and 5% trail/parking. Canopy cover is dominated by sweet gum (*Liquidambar styraciflua*), mulberry (*Morus sp.*), and black cherry (*Prunus serotina*).

The understory consists of mainly invasive species, including: Chinese privet (*Ligustrum sinense*), Japanese honeysuckle (*Lonicera japonica*), and Japanese stilt grass (*Microstegium vimineum*).

HOFFLER

Hoffler Creek Wildlife Preserve is located in Portsmouth, Virginia, and was protected starting in the mid-1990s. The make-up of the preserve as estimated by the preserve's organizers and supported by my visual estimates is about 75% forest, 20% pond, and 5% trail. Lake Ballard is a 14 ha artificial pond that lies at the center of the preserve. Additionally, the preserve borders a salt-water marsh that surrounds the northern perimeter of the preserve. The three most numerous tree species at Hoffler include: loblolly pine, common hackberry (*Celtis occidentalis*), and red maple (*Acer rubrum*). The three most numerous understory species include: southern wax myrtle (*Morella cerifera*), saltbush (*Baccharis halimifolia*), and shorebay (*Persea borbonia*).

JACOBSON

The Jacobson Tract is located in Chesapeake, Virginia. The land is owned by The Nature Conservancy (TNC) and was obtained in 2012. Per the TNC and my visual estimates, Jacobson is comprised 60% field, 30% forest, and 10% swamp. The most numerous tree species include: loblolly pine, red maple, and sweet gum, whereas the understory is dominated by greenbrier (*Smilax sp.*) and numerous native grass species.

STEPHENS

The Stephens Tract, also owned by TNC, is also located in Chesapeake, Virginia, and was created in the late 1990s. Per TNC and my visual estimates, the dominant tree species is loblolly pine, although the area is considered to be mixed coniferous-hardwood. Other common tree species include sweet gum and American sycamore (*Platanus occidentalis*). Understory species are varied over the entire tract; however, the most common species include Queen Anne's lace (*Daucus carota*), English ivy, and poison ivy (*Toxicodendron radicans*).

Detailed descriptions of the six ad-hoc sites were not taken, as they were not sampled frequently enough to gather sufficient vegetation data.

BIRD AND TICK SAMPLING

From August 2012 to August 2014, birds at 11 sites were caught, banded, and checked for ticks (Fig. 1). Birds at each site were caught using up to ten 12 m long, 2.5 m high mistnets erected for approximately 4 hr each sampling session. The majority of the sampling sessions began by local sunrise; however, some sessions were conducted from approximately 4 hr before local sunset until sunset. Birds caught close to sunset were released before it got dark. Sunrise and sunset are the most active times of day for birds, making them the most efficient times to catch birds (Daan and Aschoff 1975).

Birds caught in the nets were extracted, identified, and banded with standard United States Geological Survey (USGS) aluminum bands. Measurements taken included: mass, wing chord length, tail length, tarsus length, nare length, culmen length, body molt percentage, amount of fat, reproductive condition (presence of absence of a cloacal protuberance or brood patch), flight feather molt, flight feather wear, and skull ossification. Primary flight feathers were examined and the amount of damage, defined as the amount of chips in the feathers, estimated. Skull ossification data were collected to help determine the age of each bird. A score of 6 meant that a bird's skull was fully ossified, indicating that the individual was an adult, whereas a score of 1 signified a recently hatched bird. Younger birds have skulls that are not fully ossified (Nero 1951). Bird ages were typically categorized as juvenile (JUV), hatch-year (HY), after-hatch year (AHY), after-second year (ASY), after-third year (ATY), or unknown (U; Pyle 2008). For the purposes of this study, analyses pertaining to juvenile birds included hatch-year birds. After-second-year and ATY birds were grouped as AHY.

All birds were also categorized as male, female, or unknown (Pyle 2008). Some birds are sexually dichromatic, meaning that the males and females have different plumages, while others are sexually monochromatic and can only be reliably sexed during the breeding season when brood patches and cloacal protuberances are present (Cuthill et al. 1999, Boulton and Cassey 2012, Schut et al. 2012). Therefore, sex determination was often difficult or impossible outside of the breeding season.

Other site variables were collected upon arrival and amended as necessary throughout the sampling period: time of arrival, time when all nets were set-up, weather, and number of nets running. These variables were used to determine the number of net hours for each site in order to eliminate net-hour bias by standardizing capture rates by net hour. Disturbance was defined as any anthropogenic factor that could interrupt natural bird behavior (i.e. human presence, domestic animals such as dogs or cats walking through the study site, or bicyclists).

All ticks that were found on birds were removed using forceps and placed into individually labeled vials (one vial per parasitized bird) to be identified to species and tested for pathogens in the lab. Tick samples were kept out of direct sunlight while in the field and placed in a -20°C freezer following each day's sampling.

QUALIFYING URBANIZATION

At the beginning of the study, I ranked the permanent field sites based on qualitative estimates of urbanization (Table 1). Factors that I used to qualitatively define urbanization included estimates of percent impervious surface, percent canopy cover, and percent vegetative cover when looking at only the area within site boundaries. These approximations were based on visual surveys conducted at each site and from aerial photographs viewed in GoogleEarth (GoogleEarth 2015). Site location relative to surrounding areas (i.e. how much of the surrounding land was developed vs natural) and distance to closest cities were also considered in order to help determine how urban each site was.

QUANTIFYING URBANIZATION

In order to quantify urbanization, I used a United States Geological Survey Virginia Land Cover Map (United States Geological Survey 2011; Fig. 2). This map identifies where human populations are highest and what cover types are found throughout these areas. To assess each field site, I used a Global Positioning System device (Garmin Montana 650t, Garmin International Inc., Olathe, Kansas) to map the five permanent field sites and six additional sites in coastal southeastern Virginia.

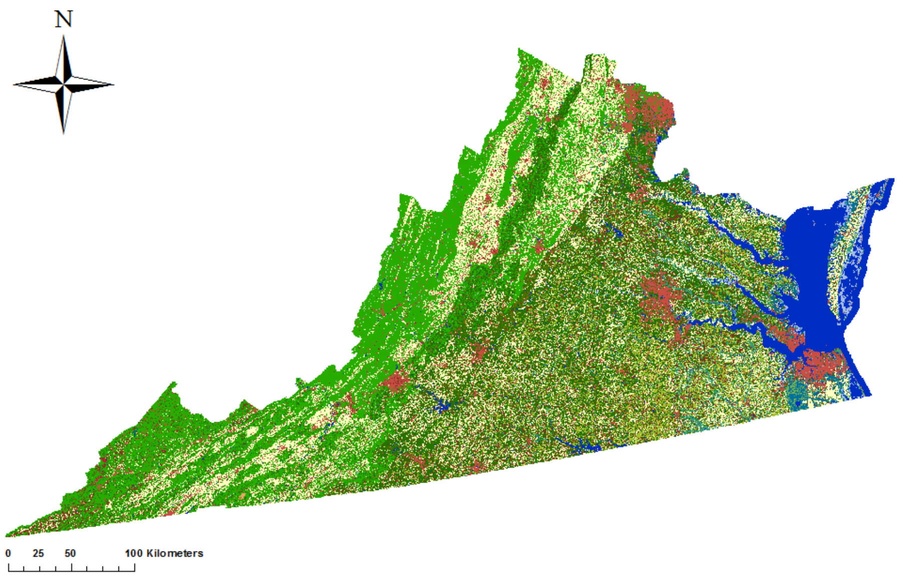

Figure 2. USGS GAP National Land Cover Map of Virginia (Homer et al. 2015; See Table 4 for full list of land cover types).

Data points for each site were added to the USGS Virginia Land Cover map using ArcGIS (version 10.3.1, ESRI, Redlands, California; Table 2), and polygons were drawn around each site to create boundaries. The centroid of each polygon was determined and used for buffer estimates.

Four fixed distance buffer zones were created around the centroids of each site: 100 m, 500 m, 1000 m, and 1500 m (Fig. 3). Individual species likely vary in their space use – some have small home ranges while others will traverse a variety of habitats over the course of a day (Haskell et al. 2002). Therefore, I used varying buffer sizes to account for the general trend of the more area covered, the more species likely can inhabit that area. The 100 m buffer was relevant at the scale of the mistnets used to capture birds, whereas the 1500 m buffer was chosen to include the scale at which organisms use space around study sites (Gergel et al. 2002). Using the extract by mask command in ArcGIS's spatial analyst extension, I was able to calculate the number of pixels of each land cover type present at each of the 11 sites. Examples of land-use/land-cover classes for the coastal southeastern Virginia included: water, developed, mechanically disturbed, mining, forest, grassland, agriculture, wetland, and non-mechanically disturbed (US Geological Survey 2011; APPENDIX A). These land cover points were consolidated into five categories: (1) tree cover, (2) ground vegetation cover, (3) all vegetation cover (includes tree and ground vegetation), (4) impervious surface, and (5) impervious surface and water cover. These cover types were used to determine the urbanization level at each site (Table 2; APPENDIX A). Combinations of the three vegetation covers (tree, ground,

Table 2. The eleven field sites used throughout this study. “Perm” = permanent site (defined as a site that was sampled consistently year-round). “Ad-hoc” = ad-hoc site (defined as a site that was sampled less than 10 times throughout the duration of the study). Listed in order of decreasing urbanization based on qualitative measurements.

Site	Size	Latitude	Longitude	Status	Years Sampled	Urban. Rank
Weyanoke	3.2	36.8733	-76.3061	Perm	2012-2014	Urban
Virginia Zoo	21.0	36.7811	-76.2762	Ad-hoc	2013-2014	Urban
Paradise	16.2	36.7990	-76.3067	Perm	2012-2014	Urban
Hidden Cove	0.8	36.8929	-76.3984	Ad-hoc	2012-2014	Suburban
Hoffler	57.5	36.7997	-76.4002	Perm	2012-2014	Suburban
York	410.5	37.2359	-76.5492	Ad-hoc	2013	Suburban
Kiptopeke	216.9	37.1694	-75.9794	Ad-hoc	2012-2013	Rural
Suffolk	152.0	36.6645	-76.5951	Ad-hoc	2013	Suburban
Jacobson	21.0	36.7997	-76.4504	Perm	2013-2014	Rural
Blackwater	404.7	36.8322	-76.8335	Ad-hoc	2012, 2014	Rural
Stephens	148.1	36.6487	-76.3498	Perm	2012-2014	Rural

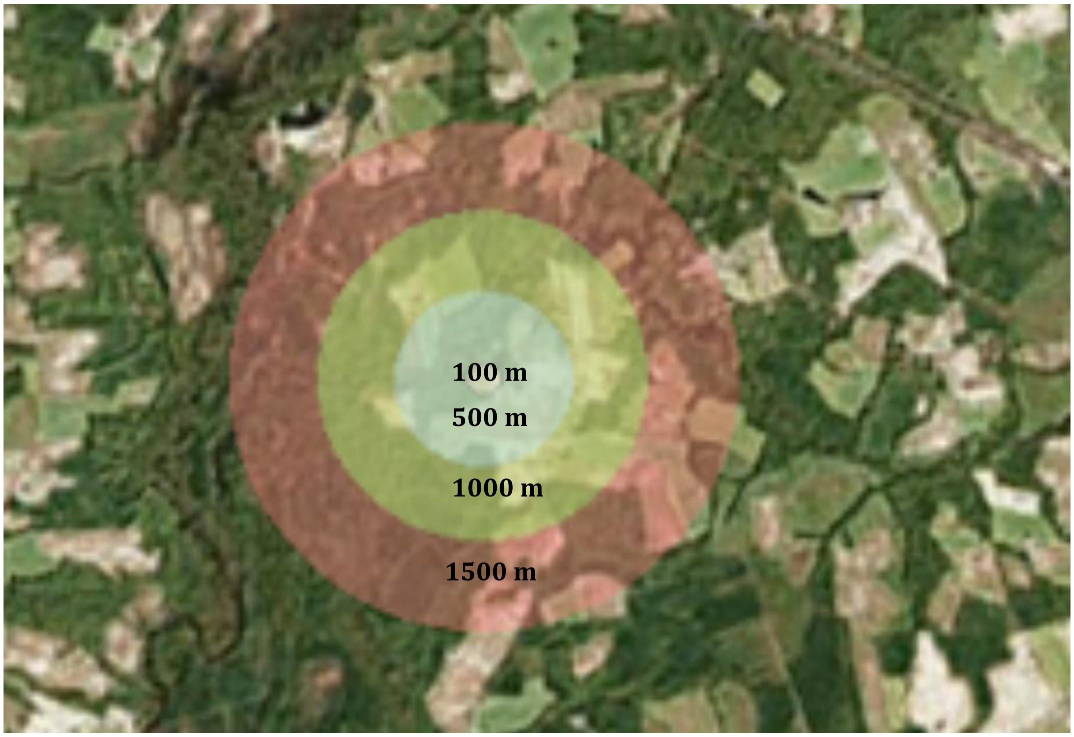

Figure 3. Example of Blackwater field site with four buffer sizes around site centroid created in ArcGIS (version 10.3.1, ESRI, Redlands, California). Background layers signify land cover type per the USGS GAP National Land Cover data (Homer et al. 2015).

all) with the two impervious surface covers (impervious surface and water + impervious surface) were used for analyses (Table 3). These five categories were consolidated from a larger list of cover types (United States Geological Survey 2011; Table 4; APPENDIX A).

Three land cover categories as listed by the USGS GAP land cover map in southeastern Virginia did not fall directly into one of the five summary categories, as they encompassed a mixture of impervious surface and vegetation cover. Therefore, percentages of each type were taken. For impervious surfaces, 20% x Class 581 (developed, open space), 49% x Class 582 (developed, low intensity), and 79% x Class 583 (developed, high intensity) were added together. For ground vegetation cover, 80% x Class 581 (developed, open space), 51% x Class 582 (developed, low intensity), and 21% x Class 583 (developed, high intensity) were added together.

These percentages were used based on the class descriptions for each land cover type (APPENDIX A). Class 581 (developed, low intensity) was described as being less than 20% impervious surface and the remainder vegetation; therefore, 20% of the class value was added to my impervious surface category and the other 80% was added to my ground vegetation cover category. Class 582 (developed, low intensity) was described as being between 20-49% impervious surface and the remainder vegetation; therefore, 49% of the class value was added to the impervious surface category and 51% to the vegetation category. Class 583 (developed, high intensity) was described as being between 50-79% impervious surface and the remainder vegetation; therefore, 79% of the class value was added to the impervious surface category and 21% to my vegetation category.

Table 3. Percent cover types by buffer size and site listed in order of decreasing urbanization. Buffer sizes were calculated by taking the centroid of each site and then adding buffers of variable size around the centroid. Data gathered by measurements using the GAP USGS National Land Cover Map for Virginia (Homer et al. 2015) and ArcGIS 10.3 (version 10.3.1, ESRI, Redlands, California).

Site	Site Status	Cover Type	100m	500m	1000m	1500m	Mean
Weyanoke	Perm	Tree	50.00	4.34	1.18	0.62	21.23
		Ground Vegetation	28.88	35.35	24.88	21.92	27.98
		All Vegetation	78.88	39.69	26.06	23.10	49.32
		Impervious	8.63	56.99	72.96	65.90	42.62
		Water+Impervious	8.62	57.68	73.22	76.77	44.98
Virginia Zoo	Ad-hoc	Tree	0.00	3.89	8.13	10.03	5.51
		Ground Vegetation	36.40	43.82	40.83	37.60	39.66
		All Vegetation	36.40	47.71	48.96	47.62	45.17
		Impervious	43.03	38.20	43.68	42.21	41.78
		Water+Impervious	43.03	39.57	44.97	44.25	42.96
Paradise	Perm	Tree	68.75	11.65	5.88	3.91	22.55
		Ground Vegetation	30.63	47.06	41.23	32.87	37.95
		All Vegetation	99.38	58.71	47.11	36.78	60.50
		Impervious	0.63	30.43	38.46	43.47	28.25
		Water+Impervious	0.63	34.66	45.20	56.87	34.34
Hidden Cove	Ad-hoc	Tree	82.86	32.53	15.57	9.41	35.09
		Ground Vegetation	0.00	15.30	29.70	31.80	19.20
		All Vegetation	82.86	47.83	45.270	41.21	54.29
		Impervious	0.00	8.48	22.44	26.16	14.27
		Water+Impervious	11.43	30.71	41.90	49.35	33.35
Hoffler	Perm	Tree	50.00	40.59	14.04	8.950	28.40
		Ground Vegetation	0.00	12.54	22.74	27.81	15.77
		All Vegetation	50.00	53.13	36.78	36.76	44.17
		Impervious	8.48	2.74	18.18	21.73	12.78
		Water+Impervious	8.63	29.28	51.43	53.41	35.69
York	Ad-hoc	Tree	100.00	61.05	49.36	52.14	65.64
		Ground Vegetation	0.00	0.34	1.53	2.93	1.20
		All Vegetation	100.00	61.39	50.88	55.07	66.84
		Impervious	0.00	0.00	0.96	3.63	1.15
		Water+Impervious	0.00	32.99	27.99	27.33	22.08

Table 3
Continued

Kiptopeke	Ad-hoc	Tree	82.86	38.26	18.61	17.47	39.30
		Ground Vegetation	5.71	9.66	6.42	5.04	6.71
		All Vegetation	88.57	47.92	25.03	22.51	46.01
		Impervious	3.00	4.21	3.14	3.00	3.34
		Water+Impervious	3.00	15.66	27.99	32.97	19.91
Suffolk	Ad-hoc	Tree	37.14	55.33	55.11	55.62	50.80
		Ground Vegetation	2.86	11.55	14.86	18.27	11.89
		All Vegetation	40.00	66.88	69.97	73.89	62.69
		Impervious	0.00	0.47	3.08	0.20	0.94
		Water+Impervious	0.00	0.47	3.08	0.20	0.94
Jacobson	Perm	Tree	6.25	42.47	44.48	43.8	34.25
		Ground Vegetation	9.38	13.90	25.89	23.14	18.08
		All Vegetation	15.63	53.37	70.38	66.94	51.58
		Impervious	0.00	5.04	11.71	9.83	6.65
		Water+Impervious	0.00	5.04	12.28	10.09	6.85
Blackwater	Ad-hoc	Tree	54.29	41.47	53.74	62.85	53.09
		Ground Vegetation	9.14	2.02	0.45	3.59	3.80
		All Vegetation	63.43	43.49	54.19	66.44	56.89
		Impervious	2.29	0.16	0.10	0.14	0.67
		Water+Impervious	8.00	0.50	0.19	0.27	2.24
Stephens	Perm	Tree	53.13	29.11	22.40	21.66	31.58
		Ground Vegetation	0.00	0.91	6.42	11.00	4.58
		All Vegetation	53.13	30.02	28.82	32.66	36.16
		Impervious	0.00	0.00	0.00	0.00	0.00
		Water+Impervious	0.00	0.00	0.00	0.00	0.00

Table 4. USGS GAP land cover types present in coastal southeastern Virginia with relative urbanization level (Homer et al. 2015; APPENDIX A). Classes not used in AICc analyses have N/A listed as their cover type.

Class	Class Name	Cover Type
38	Evergreen Plantations or Managed Pine	Tree
103	Atlantic Coastal Plain Dry and Dry-Mesic Oak Forest	Tree
120	Atlantic Coastal Plain Mesic Hardwood and Mixed Forest	Tree
241	Atlantic Coastal Plain Nonriverine Swamp and Wet Hardwood Forest - Taxodium/Nyssa Modifier	Tree
242	Atlantic Coastal Plain Nonriverine Swamp and Wet Hardwood Forest - Oak Dominated Modifier	Tree
246	Northern Atlantic Coastal Plain Basin Swamp and Wet Hardwood Forest	Tree
399	Atlantic Coastal Plain Peatland Pocosin	N/A
403	Atlantic Coastal Plain Northern Fresh and Oligohaline Tidal Marsh	N/A
450	Atlantic Coastal Plain Northern Tidal Salt Marsh	N/A
556	Cultivated Cropland	N/A
557	Pasture/Hay	N/A
567	Harvested Forest - Grass/Forb Regeneration	Ground Vegetation
568	Harvested Forest - Shrub Regeneration	Ground Vegetation
575	Disturbed/Successional - Shrub Regeneration	Ground Vegetation
578	Open Water (Brackish/Salt)	Water
579	Open Water (Fresh)	Water
580	Quarries, Mines, Gravel Pits and Oil Wells	Impervious
581	Developed, Open Space	Impervious/Ground Vegetation
582	Developed, Low Intensity	Impervious/Ground Vegetation
583	Developed, Medium Intensity	Impervious/Ground Vegetation
584	Developed, High Intensity	Impervious

STATISTICAL ANALYSES

In order to determine the effects of urbanization on tick parasitism rates, I used logistic regression in SPSS Statistics 21 (IMB Corp. 2012) and a test of equal or given proportions in R (Version 3.2.1; Burnham and Anderson 2002). The assumptions for logistic regression included: (1) dependent variable is dichotomous, (2) at least one independent variable must be either continuous or categorical, (3) observations are independent of one another, and (4) there is a relatively linear relationship between continuous independent variables and dependent variables (Menard 2002). Data were checked to ensure that they met the assumptions for logistic regression. The assumption of independence of observations was not fully met, as recaptured birds were used in analyses. I used recaptures, as all ticks were removed from each individual before release, and therefore, if a bird was recaptured, it had an equal opportunity to be parasitized or not. Additionally, all recaptures occurred at least two weeks apart, enough time for any ticks that may have been missed to fall-off before recapture.

In order to determine what variables related to urbanization were the best predictors of tick parasitism, I used AICc (Akaike Information Criterion for small sample sizes) ranking in the MuMIn package in R (Version 3.2.1; Burnham and Anderson 2002). Categorical variables for both logistic regression and AIC analyses included: day of year (DOY), month, year, season, site, bird species, species richness over the course of the study for each site, and tick presence on a bird (Yes or No). Season was defined as: winter (December – February, DOY 335 to 365 and 1 to 59), spring (March-May; DOY 60 to 152), summer (June – August; DOY 153 to 243), or fall (September-November; DOY 244 to 334).

Forty-four candidate models were included with varying combinations of the three vegetation cover categories and two impervious surface categories for each of the four buffer zones (100 m, 500 m, 1000 m, and 1500 m; Tables 4), season, and species richness. Multicollinearity was tested for all models using the variance inflation factor (VIF) in the CAR package in R (Fox and Weisberg 2011). Based on the VIF factors, four of these models (trees + impervious surface 500 m buffer, ground vegetation + impervious surface 500 m buffer, trees + impervious surface 1000 m buffer, and trees + impervious surface 1500 m buffer) were eliminated due to multicollinearity issues, represented by variables that were correlated above 0.7 or below -0.7 in the same model (Anderson et al. 2001).

RESULTS

A total of 1468 captures of birds representing 74 species occurred in 6774.38 net hours over 245 netting sessions for an overall netting success rate of 21.2 captures per 100 net hours at the five permanent sites (Weyanoke, Paradise, Hoffler, Jacobson, and Stephens) used for these analyses. Birds were also caught at six ad-hoc sites (Virginia Zoo, York, Hidden Cove, Kiptopeke, Blackwater, and Suffolk). When including both permanent and ad-hoc sites, a total of 1886 captures representing 76 species occurred in 7963.38 net hours over 289 netting sessions for an overall netting success rate of 23.7 captures per 100 net hours.

Of the 1886 birds caught at all sites (both permanent and ad-hoc), 18.27% of birds were recaptured at a later point in the study. The five most abundant species (*n>70*) captured were Northern Cardinal (*Cardinalis cardinalis*, *n=255*), Carolina Wren (*Thyrothorus ludovicianus*, *n=160*), White-throated Sparrow (*Zonotrichia albicollis*, *n=129*), Gray Catbird (*Dumetella carolinensis*, *n=89*), and American Robin (*Turdus migratorius*, *n=73*).

Over the duration of the study for all eleven sites, 943 ticks were collected from the 1886 birds caught. Of all birds caught, 3.21% of birds captured were parasitized by at least one tick. When considering only bird species where at least 70 individuals were caught, the five most abundant bird species captured with ticks were: Northern Cardinal (*n=255*; 3.92%); Carolina Wren (*n=160*; 38.75%), Gray Catbird (*n=82*; 2.44%), American Robin (*n=73*; 9.59%), and Yellow-rumped Warbler (*Setophaga coronata ; n=71*; 1.41%; Fig. 4).

For the following analyses, I did not use ad-hoc sites because these sites were only sampled irregularly, and therefore, little data were gathered for them. Later, however, I compare landscape metrics associated with ad-hoc sites to permanent sites in order to examine urbanization patterns across a wider range of sites. All years in which birds were sampled at permanent field sites (2012, 2013, 2014) were combined because there was no significant year effect of tick parasitism across permanent field sites (Wald=4.575, df=2, P=0.102).

QUALITATIVE SITE URBANIZATION LEVELS

My qualitative estimates based on visual approximations and estimates from those who manage each site, resulted in permanent sites being ordered in the

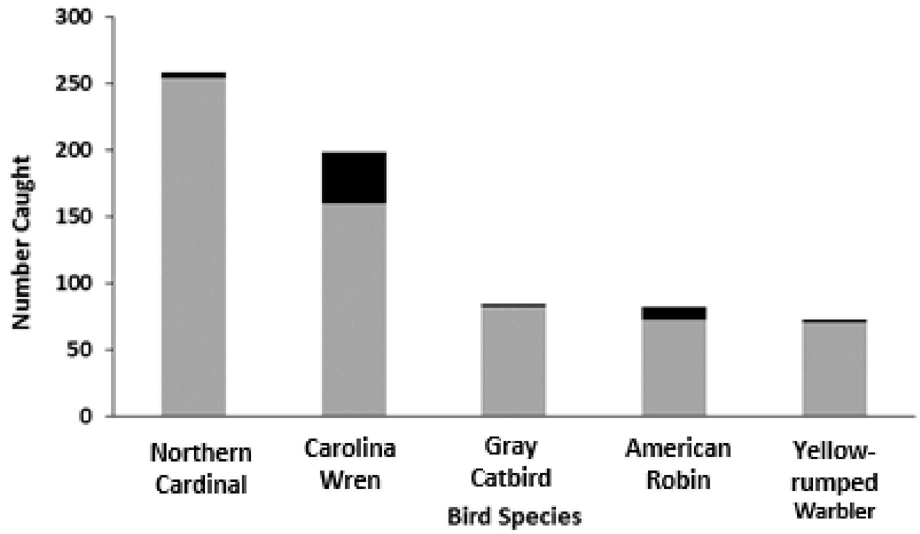

Figure 4. Most common bird species with ticks caught at all permanent sites. Black represents the percent caught parasitized by ticks.

following order of decreasing urbanization: Weyanoke, Paradise, Hoffler, Jacobson, and Stephens (Table 2). Weyanoke was ranked as most urban due to its proximity to the heart of the city of Norfolk and because surrounding areas included suburban neighborhoods and industrial train yards. Paradise was ranked as second most urban. It too is close to suburban neighborhoods and is next to an industrial paper plant; however, Paradise has noticeably less impervious surfaces surrounding the perimeter of the site than Weyanoke. Hoffler was ranked as the middle site (suburban) due to its proximity to suburban neighborhoods but high percent canopy cover. It consists of much denser forested areas and edge habitat than either Weyanoke or Paradise. Jacobson was ranked next, as the second most rural site. It was ranked as such because it is located in the center of a neighborhood; however, the neighborhood surrounding Jacobson is much less developed than the other neighboring areas discussed previously. Jacobson also has a high proportion of vegetation and canopy cover and consists of a mixture of forest and fields. Stephens was ranked as the most rural site. Very few houses and developed areas are adjacent to this site, as it is surrounded primarily by agricultural fields and consists of dense trees and vegetative cover. Because of these rankings, Weyanoke and Paradise were both labeled as urban sites; Hoffler was suburban; Jacobson and Stephens were both rural.

When including the ad-hoc sites, I qualitatively ranked sites in the following order from most to least urbanized: Weyanoke, Virginia Zoo, Paradise, Hidden Cove, Hoffler, York, Kiptopeke, Suffolk, Jacobson, Blackwater, and Stephens. The Virginia Zoo was ranked after Weyanoke and before Paradise as it is located in the heart of Norfolk, close to very urban areas, has high visitation rates by tourists, and includes a well-manicured landscape. Because it is surrounded by grassy fields and the Lafayette River, I considered it less urbanized than Weyanoke, yet more urbanized than Paradise, as Paradise is not manicured. Hidden Cove is a property within a suburban neighborhood, 1.43 km from Hoffler. Due to its proximity to a local wildlife preserve, it was considered less urbanized than Paradise. The York site comprised open field and forest. It is surrounded by some suburban areas but also by industrial areas and therefore was considered more urbanized than Hoffler. Kiptopeke is a state park and consists of forested areas, beach, and fields. The areas surrounding Kiptopeke are primarily suburban and farmland. Because it is a public park, it was deemed more urbanized than the sites that were on private land, as for this study, privately-owned land tended to be less manicured and altered than publically-owned land. Suffolk was considered less urbanized than Kiptopeke because it is private forested land with several fields fragmenting the forest and is surrounded by mostly agricultural fields. Blackwater consists of open fields and pine forests and is owned by Old Dominion University. Because no suburban areas surround Blackwater, it was ranked more rural than Jacobson; however, because parts of Blackwater are maintained, it was ranked less rural than Stephens.

QUANTITATIVE SITE URBANIZATION LEVELS

In order to independently rank sites by level of urbanization, I ranked the five permanent field sites based on quantitative estimates as well. Using land cover datasets, I determined the proportion tree cover, ground vegetation cover, all vegetation cover, impervious surface, and impervious surface plus water cover for all sites (Table 3; Figs. 5, 6, 7) and ranked the sites based on the mean percent impervious surface, as other studies have found that percent impervious surface is a good indicator of urbanization (Arnold and Gibbons 1996, Morse et al. 2003; Figs. 5, 6); therefore, I ranked the five permanent field sites in the following order of decreasing urbanization, with the percentages in parentheses indicating percent impervious surface: Weyanoke (51.12%%), Paradise (25.33%), Hoffler (12.29%), Jacobson (7.20%), and Stephens (0.00%; Fig. 6). Qualitative estimates of urbanization matched the quantitative rankings for the 5 permanent field sites (Table 2). When adding in ad-hoc field sites, I ranked the sites in the following order of decreasing urbanization based on percent impervious cover: Weyanoke (51.12%), Virginia Zoo (41.36%), Paradise (25.33%), Hidden Cove (19.03%), Hoffler (11.53%), Jacobson (7.19%), York (1.53%), Suffolk (1.25%), Blackwater (0.67%), Kiptopeke (3.45%), Blackwater (0.13%), and Stephens (0.00%; Table 3).

IMPERVIOUS SURFACE HYPOTHESIS

A suite of nested additive candidate models were ranked using AICc to determine what landscape and abiotic predictor variable(s) were most supportive (Tables 5). When looking at models using only buffer data, the percentages for tree,

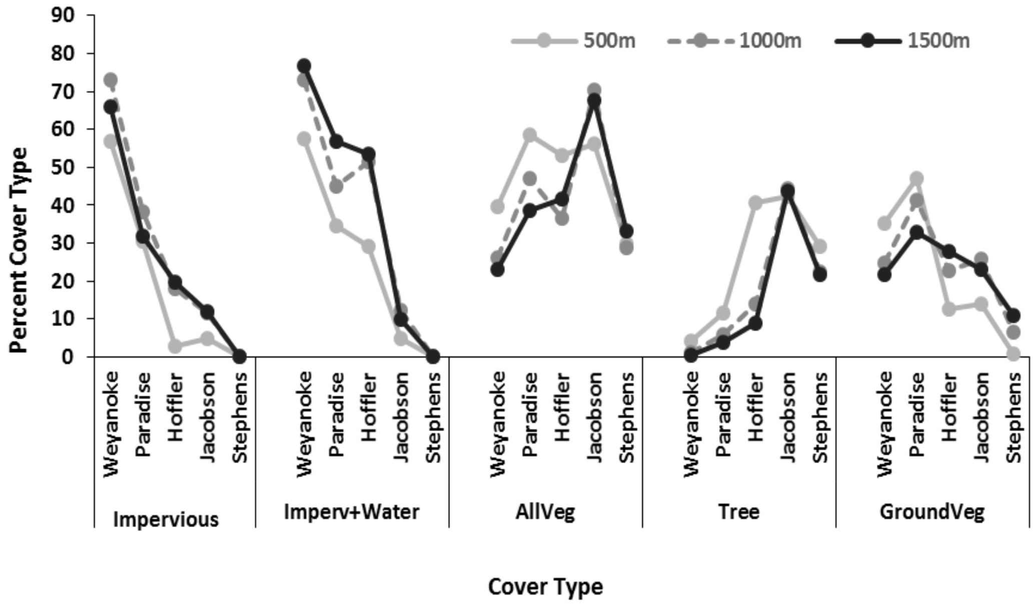

Figure 5. Percent cover types by site at 500 m, 1000 m, and 1500 m buffers.

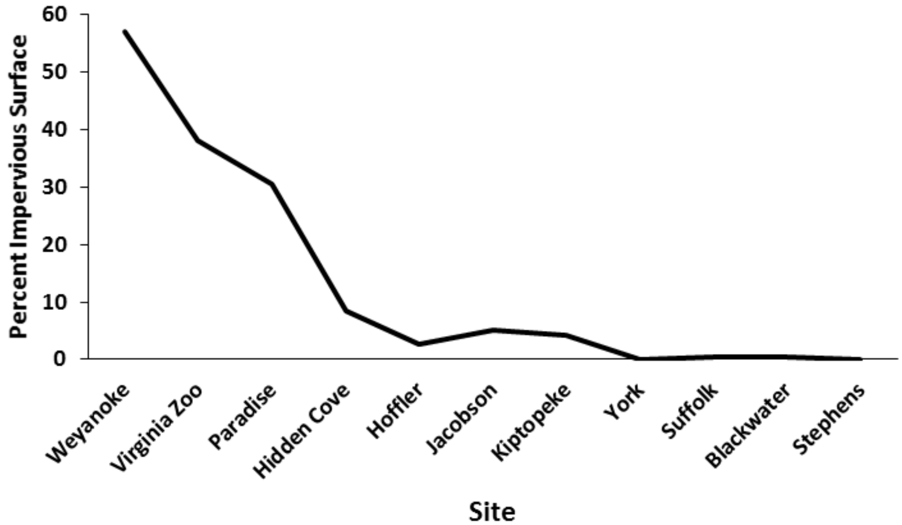

Figure 6. Percent impervious surface cover is shown across all field sites in order from most urban to least urban.

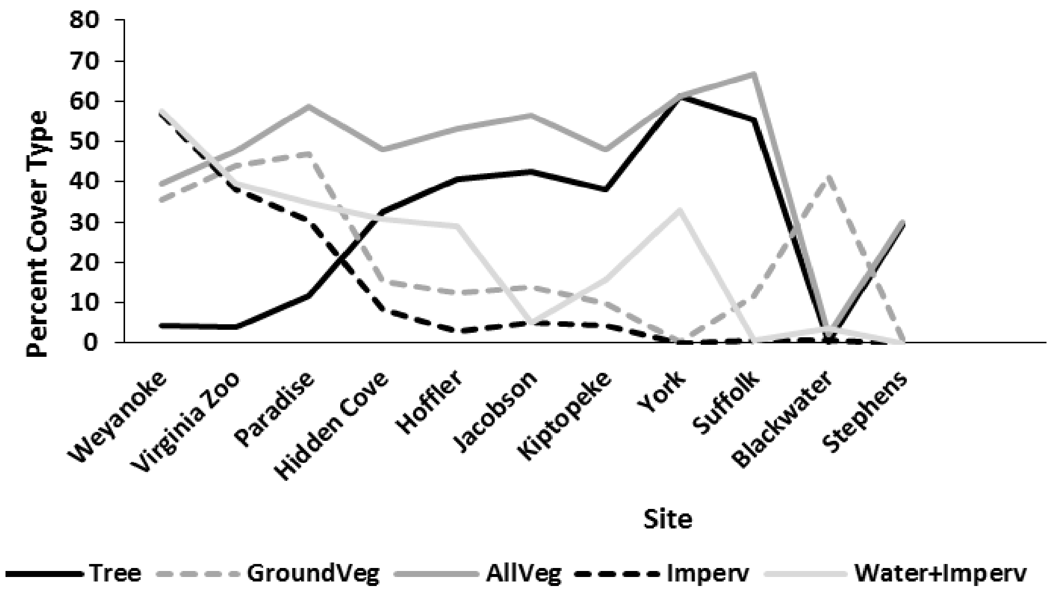

Figure 7. Percent tree, ground vegetation, all vegetation, impervious surface, and impervious surface + water covers at the 500 m buffer are presented across all sites in order of most urban to least urban.

Table 5. AIC values and model rankings for all models from all permanent sites.

Model Name	df	AICc	ΔAICc	AICcWt	LL
Impervious Surface 500 m buffer	2	870.5	0.00	0.721	-433.26
All Vegetation + Impervious Surface 500 m buffer	3	872.5	2.01	0.264	-433.26
Ground Vegetation + Impervious Surface 1500 m buffer	3	878.9	8.34	0.011	-436.42
Ground Vegetation + Impervious Surface 100 m buffer	3	883.0	12.49	0.001	-438.50
Ground Vegetation + (Water + Impervious Surface) 100 m buffer	3	883.1	12.56	0.001	-438.53
Ground Vegetation + Impervious Surface 1000 m buffer	3	887.7	17.13	0.000	-440.82
All Vegetation + Impervious Surface 1000 m buffer	3	888.7	18.22	0.000	-441.36
Impervious Surface 1000 m buffer	2	888.9	18.42	0.000	-442.47
Impervious Surface 1500 m buffer	2	892.1	21.62	0.000	-444.07
Ground Vegetation 500 m buffer	2	892.9	22.40	0.000	-444.46
Ground Vegetation + Impervious Surface 500 m buffer	3	893.2	22.68	0.000	-443.60
Ground Vegetation + (Water + Impervious Surface) 500 m buffer	3	893.2	22.68	0.000	-443.60
All Vegetation + Impervious Surface 1500 m buffer	3	893.5	23.01	0.000	-433.76
Trees + (Water + Impervious Surface) 500 m buffer	3	894.2	23.65	0.000	-444.08
Ground Vegetation 100 m buffer	2	902.4	31.87	0.000	-449.19
Water + Impervious Surface 500 m buffer	2	931.9	61.36	0.000	-463.94
All Vegetation + (Water + Impervious Surface) 500 m buffer	3	933.6	63.05	0.000	-463.78
Trees 500 m buffer	2	939.2	68.65	0.000	-467.58
Ground Vegetation + (Water + Impervious Surface) 1000 m buffer	3	957.0	86.50	0.000	-475.50
Water + Impervious Surface 1500 m buffer	2	955.1	84.58	0.000	-475.55
Trees + (Water + Impervious Surface) 1500 m buffer	3	956.7	86.14	0.000	-475.32
All Vegetation + (Water + Impervious Surface) 1500 m buffer	3	956.8	86.23	0.000	-475.37

Table 5 Continued

Ground Vegetation + (Water + Impervious Surface) 1500 m buffer	3	957.0	86.50	0.000	-475.50
Trees + (Water + Impervious Surface) 1000 m buffer	3	959.6	89.08	0.000	-476.79
All Vegetation 100 m buffer	2	959.6	89.09	0.000	-477.80
All Vegetation + Impervious Surface 100 m buffer	3	960.3	89.74	0.000	-477.12
All Vegetation + (Water + Impervious Surface) 100 m buffer	3	960.4	89.86	0.000	-477.18
Water + Impervious Surface 1000 m buffer	2	964.9	94.41	0.000	-480.46
All Vegetation + (Water + Impervious Surface) 1000 m buffer	3	966.8	96.26	0.000	-480.38
Ground Vegetation 1000 m buffer	2	968.8	98.29	0.000	-482.40
Trees 1000 m buffer	2	983.5	113.00	0.000	-489.76
Trees 1500 m buffer	2	991.9	121.42	0.000	-493.97
Ground Vegetation 1500 m buffer	2	1005.8	135.3	0.000	-500.89
Season + Species Richness	5	1017.0	146.5	0.000	-503.50
Season	4	1019.5	149.02	0.000	-505.58
Trees +Impervious Surface 100 m buffer	3	1026.8	156.27	0.000	-510.39
Trees + (Water + Impervious Surface) 100 m buffer	3	1027.2	156.66	0.000	-510.58
Trees 100 m buffer	2	1030.5	160.02	0.000	-513.27
All Vegetation 1500 m buffer	2	1035.4	164.85	0.000	-515.68
All Vegetation 500 m buffer	2	1045.2	174.70	0.000	-520.61
Impervious Surface 100 m buffer	2	1049.5	179.02	0.000	-522.77
Water + Impervious Surface 100 m buffer	2	1050.1	179.60	0.000	-523.05
Species Richness	2	1049.8	179.03	0.000	-522.90
Water + Impervious Surface 1000 m buffer	2	1050.1	179.58	0.000	-523.05
All Vegetation 1000 m buffer	2	1059.1	188.54	0.000	-527.53
Intercept	1	1059.5	189.03	0.000	-528.77

ground vegetation, all vegetation, impervious, and water + impervious were calculated in GIS for each site at each buffer size, and these variables along with site, season, and species richness were used in candidate models as predictors of tick parasitism. Using all permanent field sites, I found that impervious cover 500m was the best model for predicting reduced tick parasitism on birds. Model averaging showed that impervious surface cover at the 500 m buffer is the best predictor of reduced tick parasitism (Table 6). Using these impervious surface cover parameter estimates gathered using AIC analyses, I compared the data for the six ad-hoc sites with the five permanent sites used in the AIC comparisons (Fig. 8). As percent impervious surface increased, the proportion of birds with ticks decreased (Fig. 8). The six ad-hoc sites generally also showed an association of increasing parasitism rates associated with a decrease in impervious surface. The outliers along the model-predicted curve were Kiptopeke and Blackwater – these sites exhibited a much higher proportion of birds parasitized relative to percent impervious surface than expected.

In order to reduce the bias that sites with very few to no ticks were having on trends, I eliminated Weyanoke and Paradise for a second set of analyses, as no ticks were collected from Weyanoke and only three from Paradise over the duration of the study. After doing so, I found that season was the best model for predicting tick parasitism of birds when looking at AIC values for both buffer and all other models (Table 7). Season + Species Richness (ΔAICc = 0.33) was also a well-supported model for predicting tick parasitism of birds. The model-averaged estimates indicate

Table 6: AIC model averages using data from all permanent sites.

Parameter	**ModAvg**	**Unconditional Standard Error**
Intercept	-1.11E-01	2.37E+00
Impervious Surface 500 m buffer	-1.14E-01	2.23E-02
All Vegetation 500 m buffer	-3.11E-06	4.28E-03
Ground Vegetation 1500 m buffer	1.06E-03	1.04E-02
Impervious Surface 1500 m buffer	-1.24E-03	1.18E-02
Ground Vegetation 100 m buffer	-2.98E-04	5.71E-03
Impervious Surface 100 m buffer	-1.36E-04	3.72E-03
Water + Impervious Surface 100 m buffer	-1.29E-04	3.59E-03
Ground Vegetation 1000 m buffer	4.70E-06	4.64E-04
Impervious Surface 1000 m buffer	-2.37E-05	1.43E-03
All Vegetation 1000 m buffer	6.47E-07	8.70E-05
Ground Vegetation 500 m buffer	-1.41E-06	3.33E-04
Water + Impervious Surface 500 m buffer	-3.06E-07	1.02E-04
All Vegetation 1500 m buffer	3.42E-08	2.04E-05
Trees 500 m buffer	2.98E-07	1.31E-04
Water + Impervious Surface1000 m buffer	-5.72E-20	3.41E-11
Water + Impervious Surface 1500 m buffer	-2.13E-20	2.56E-11
Trees 1500 m buffer	7.68E-22	3.66E-12
Trees 1000 m buffer	6.70E-22	3.95E-12
All Vegetation 100 m buffer	-2.40E-21	8.62E-12
Trees 100 m buffer	-3.16E-36	2.50E-19
Season (Winter + Spring)	-4.75E-01	0.327342
Season (Winter + Summer)	3.13E-01	0.303263
Season (Winter + Fall)	9.36E-01	0.285096
Species Richness	4.19E-02	0.030797

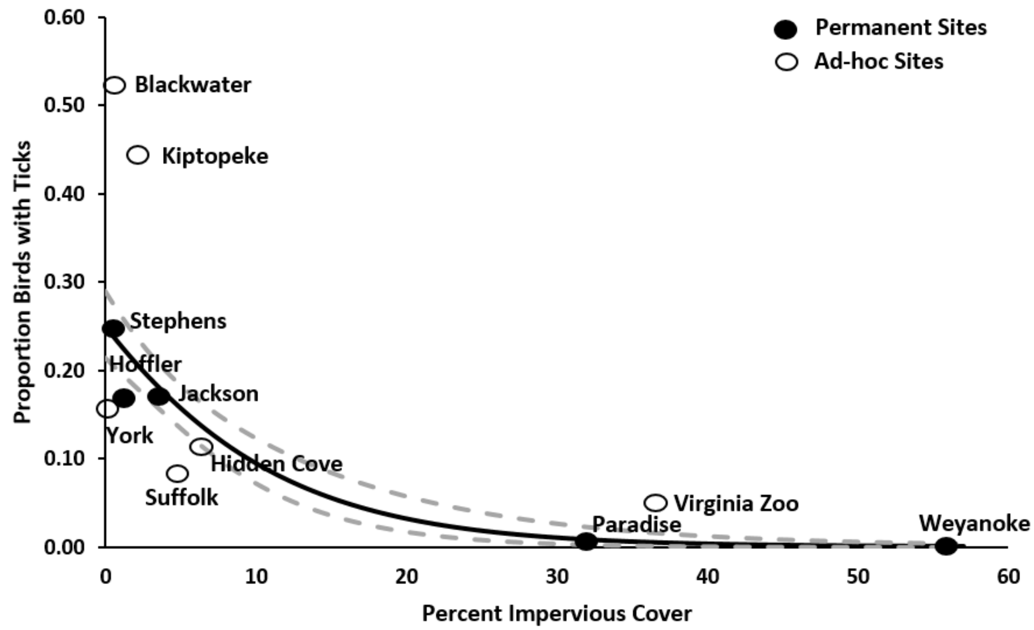

Figure 8. Model averaged proportion of birds with ticks relative to percent impervious surface at the 500 m buffer. Dotted lines indicate unconditional standard errors around predictions.

Table 7: AIC values and model rankings for all models from Hoffler, Jacobson, and Stephens.

Model Name	df	AICc	ΔAICc	AICcWt	LL
Season	4	815.3	0.00	0.282	-403.64
Season + Species Richness	5	815.7	0.33	0.239	-402.79
Ground Vegetation 500 m buffer	2	823.3	15.34	0.065	-414.13
Impervious Surface 1000 m buffer	2	830.7	15.36	0.065	-413.33
Impervious Surface 1500 m buffer	2	830.7	15.48	0.063	-413.33
Ground Vegetation 1500 m buffer	2	830.8	15.98	0.061	-413.40
Water + Impervious Surface 1000 m buffer	2	831.3	16.19	0.047	-413.65
Water + Impervious Surface 1500 m buffer	2	831.5	16.26	0.043	-413.75
Water + Impervious Surface 500 m buffer	2	831.6	16.94	0.029	-413.79
All Vegetation 500 m buffer	2	832.4	17.04	0.028	-414.18
Water + Impervious Surface 100 m buffer	2	832.5	17.12	0.027	-414.22
Impervious Surface 100 m buffer	2	832.5	17.12	0.027	-414.22
Trees 500 m buffer	2	832.5	17.14	0.026	-414.23
Ground Vegetation 1000 m buffer	2	832.6	17.28	0.020	-414.30
Trees + Impervious Surface 100 m buffer	3	832.6	17.29	0.000	-413.30
Trees + (Water + Impervious Surface) 100 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + (Water + Impervious Surface) 100 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + Impervious Surface) 100 m buffer	3	832.6	17.29	0.000	-413.30
Trees + (Water + Impervious Surface) 500 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + (Water + Impervious Surface) 500 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + Impervious Surface 500 m buffer	3	832.6	17.29	0.000	-413.30
Trees + (Water + Impervious Surface) 1000 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + Impervious Surface 1000 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + (Water + Impervious Surface) 1000 m buffer	3	832.6	17.29	0.000	-413.30

Table 7 Continued

Trees + (Water + Impervious Surface) 1500 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + Impervious Surface 1500 m buffer	3	832.6	17.29	0.000	-413.30
Ground Vegetation + (Water + Impervious Surface) 1500 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + (Water + Impervious Surface) 1500 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + (Water + Impervious Surface) 1500 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + Impervious Surface 100 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + (Water + Impervious Surface) 100 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + (Water + Impervious Surface) 500 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + Impervious Surface 1000 m buffer	3	832.6	17.29	0.000	-413.30
All Vegetation + (Water + Impervious Surface) 1000 m buffer	3	832.6	17.29	0.000	-413.30
Impervious Surface 500 m buffer	2	835.0	19.63	0.000	-415.47
Intercept	1	835.9	20.59	0.000	-416.96
Trees 1500 m buffer	2	836.9	21.61	0.000	-416.46
Trees 1000 m buffer	2	837.4	22.07	0.000	-416.69
All Vegetation 1000 m buffer	2	837.5	22.20	0.000	-416.75
Species Richness	2	837.6	22.28	0.000	-416.80
All Vegetation 1500 m buffer	2	837.8	22.43	0.000	-416.87
All Vegetation 100 m buffer	2	837.8	22.51	0.000	-416.91
Trees 100 m buffer	2	837.9	22.54	0.000	-416.92
Ground Vegetation 100 m buffer	2	837.9	22.60	0.000	-416.95

that the comparison between the winter and spring seasons was the best predictor of tick parasitism, followed by the comparison between the winter and summer seasons being the second best predictor for tick parasitism (Table 8). In other words, when comparing winter to other seasons, the comparison between winter and both spring and summer were better predictors of tick parasitism than that between winter and fall.

When addressing tick proportion of birds by each season, the least number of birds were parasitized during the winter, followed by the spring and summer. The smallest proportion of birds with ticks were caught during the winter, whereas the highest proportion of birds with ticks were caught during the fall (Fig. 9), suggesting that the fall would be the best season predictor for parasitism. This trend is also shown when looking at day-of-year figures (Fig. 10). Additionally, the second highest ranked models suggested a decrease in the proportion of birds with ticks as avian species diversity increased (Fig. 11).

ENVIRONMENTAL CONSTRAINT HYPOTHESIS

The environmental constraint hypothesis states that birds in urban areas are less likely to be parasitized by ticks than those found in rural areas. To address this question, I used two approaches. The first considered only species where at least 10 individuals were caught per site and at least one individual was parasitized by at least one tick at each of the five permanent sites. This limited the analyses to only three species of birds: Northern Cardinal, Carolina Wren, and White-throated Sparrow (Fig. 12). Since there was no year effect on the data pertaining to these species (Wald=4.042, df=2, P=0.133), I combined data from all years (2012, 2013,

Table 8: AIC model averages using data from Hoffler, Jacobson, and Stephens.

Parameter	ModAvg	Unconditional Standard Error
Intercept	-1.75E+00	0.438917
Season (Winter + Spring)	-5.93E-02	0.325154
Season (Winter + Summer)	6.58E-01	0.313344
Season (Winter + Fall)	1.07E+00	0.297167
Species Richness	-1.67E-02	0.026357
Impervious Surface 1500 m buffer	-3.47E-03	0.043255
Impervious Surface 1000 m buffer	-3.49E-03	0.015188
Ground Vegetation 1500 m buffer	-2.01E-03	0.054832
Water + Impervious Surface 1000 m buffer	-1.16E-03	0.004464
Water + Impervious Surface 1500 m buffer	-1.07E-03	0.005825
Water + Impervious Surface 500 m buffer	-1.66E-03	0.008113
Ground Vegetation 500 m buffer	-1.48E-03	0.018730
All Vegetation 500 m buffer	-1.76E-03	0.019694
Water + Impervious Surface 100 m buffer	-5.75E-03	0.023031
Impervious Surface 100 m buffer	-5.85E-03	0.023419
Trees 500 m buffer	-9.03E-04	0.014603
Ground Vegetation 1000 m buffer	-7.13E-04	0.020097
Trees 100 m buffer	4.23E-04	0.004810
Ground Vegetation 100 m buffer	-1.56E-03	0.024308
Impervious Surface 500 m buffer	3.45E-03	0.151912
Trees 1000 m buffer	-1.62E-04	0.009090
Trees 1500 m buffer	-1.62E-04	0.009090
All Vegetation 1500 m buffer	-1.17E-04	0.007373
All Vegetation 100 m buffer	3.93E-04	0.006039
All Vegetation 1000 m buffer	-7.93E-05	0.006059

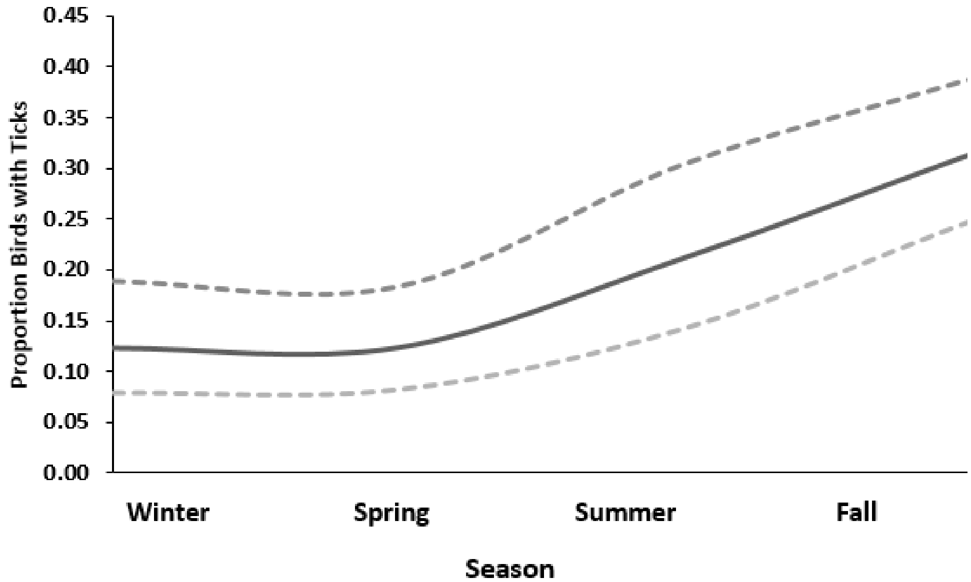

Figure 9. Model averaged proportion of birds with ticks as a function of season. Dotted lines indicate unconditional standard errors around predictions.

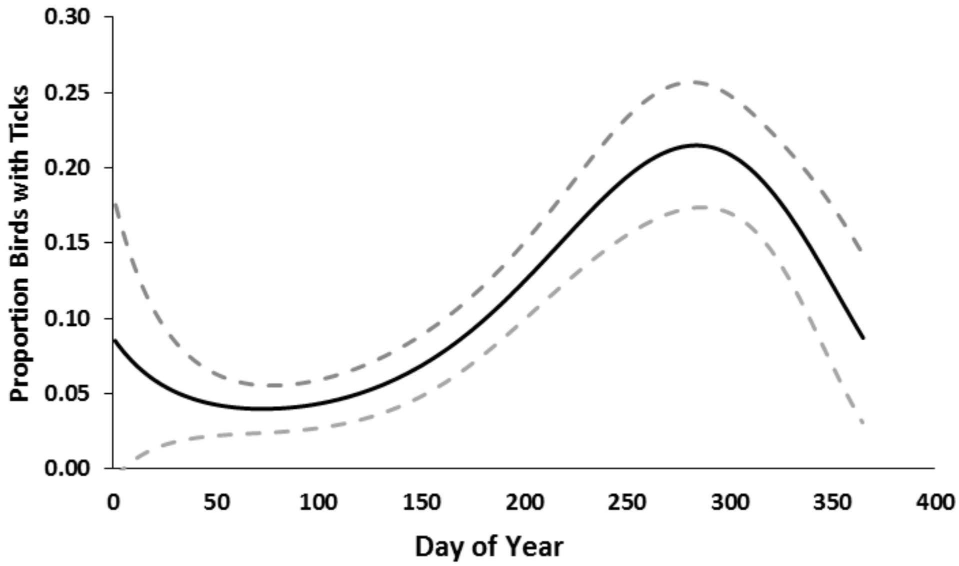

Figure 10: Model averaged proportion of birds with ticks relative to day-of-year. Dotted lines indicate unconditional standard errors around predictions.

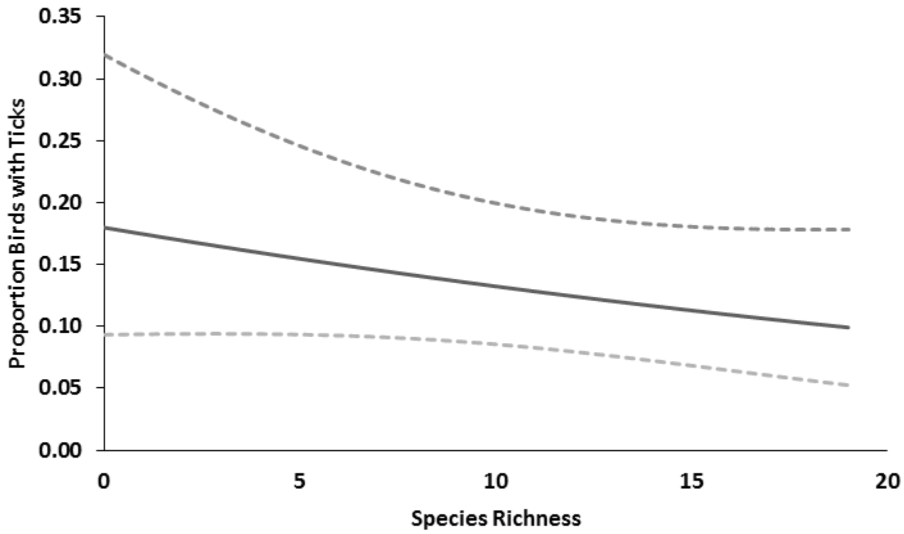

Figure 11. Model averaged proportion of birds with ticks relative to avian species richness. Dotted lines indicate unconditional standard errors around predictions.

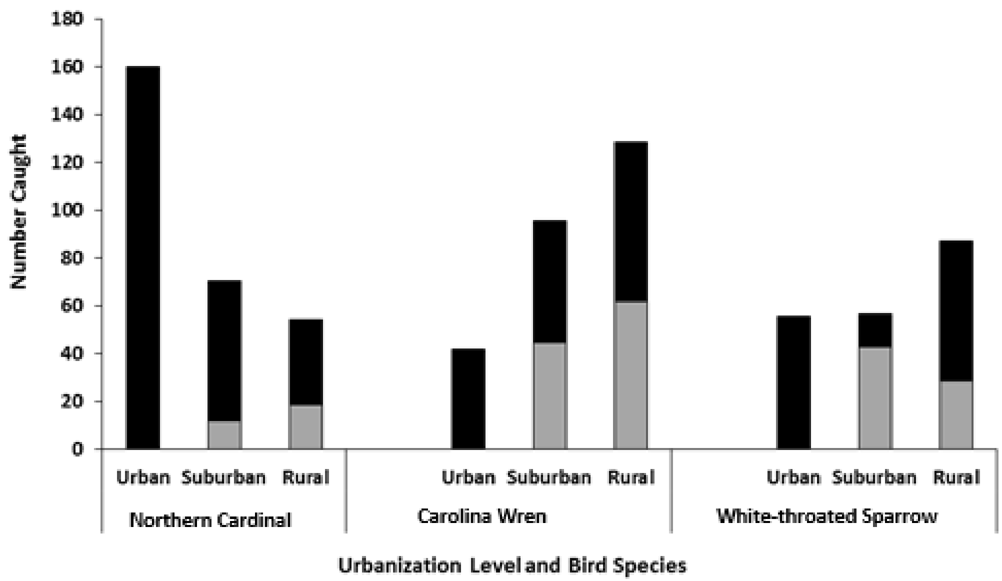

Figure 12. Three bird species caught at all permanent sites. Number caught and number with ticks presented. The subset of individuals found parasitized by ticks is indicated in black.

2014) to run this species-specific analysis. There was a significant effect of how urban a site was based on tick parasitism (Wald=26.910, df=2, P<0.001). Birds caught at rural sites were more likely to be parasitized by ticks than those caught at urban sites (Wald=25.533, df=1, Exp(B)=168.640, P<0.001) but not at suburban sites (Wald=2.800, df=1, Exp(B)=1.533, P=0.094). Birds caught at suburban sites were more likely to be parasitized by ticks than birds caught at urban sites (Wald=8.746, df=1, Exp(B)=1.612, P=0.003; Fig. 13). The second approach examined all bird species where at least 10 individuals were caught among all sites. At least one of the birds for each species had to have been parasitized by at least one tick; however, this approach did not require that each individual species occurs at all sites, as was performed in the first approach.

This limited analyses to twelve bird species: Carolina Wren, American Robin, Gray Catbird, Hermit Thrush (*Catharus guttatus*), Northern Mockingbird (*Mimus polyglottos*), Brown Thrasher (*Toxostoma rufum*), Yellow-rumped Warbler, Common Yellowthroat (*Geothlypis trichas*), Dark-eyed Junco (*Junco hyemalis*), Song Sparrow (*Melospiza melodia*), White-throated Sparrow, and Northern Cardinal. There was no year effect when addressing tick parasitism for these species (Wald=4.575, df=2, P=0.102), so data from all years were combined. Again, there was a significant difference in tick parasitism rates based on urbanization classification (Wald=45.955, df=2, P<0.001). Birds were more commonly parasitized by ticks at rural sites than at urban sites (Wald=44.929, df=1, Exp(B)=52.632, P<0.001; Fig. 13). Birds were also more likely to be parasitized at suburban sites than at urban sites (Wald=36.696, df=1, Exp(B)=37.378, P<0.001). However, no difference in tick

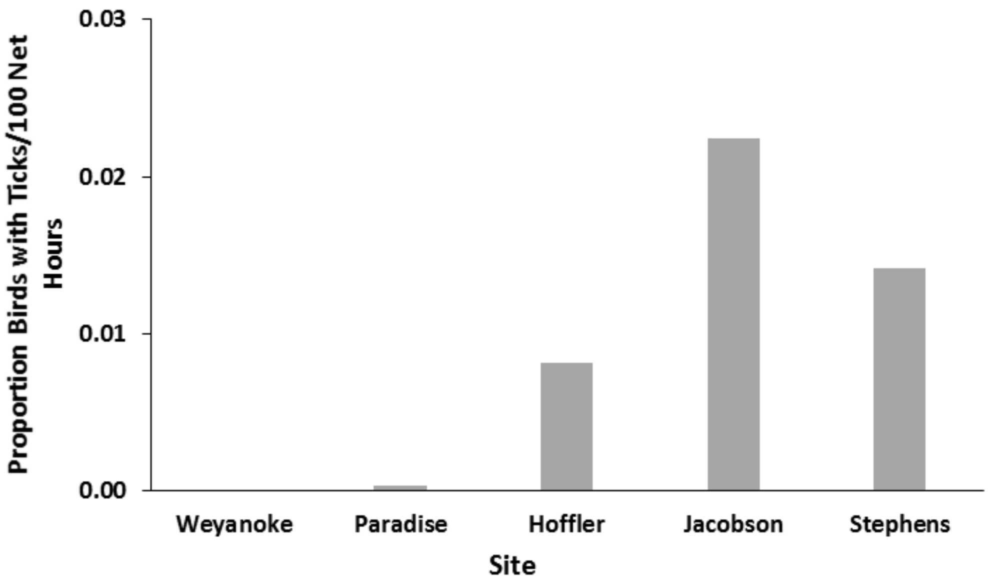

Figure 13. Proportion of birds with ticks per 100 net hours by site. Weyanoke and Paradise were urban. Hoffler was suburban. Jacobson and Stephens were rural.

parasitism was found between rural and suburban sites (Wald=3.271, df=1, Exp(B)=1.403, P=0.710; Fig. 13).

HOST CONSTRAINT HYPOTHESIS

The host constraint hypothesis posits that ticks exhibit less avian-host preference in urban areas than in rural areas due to decreased avian species richness (Fig. 10). Stephens, the most rural site, had 37 species of birds, 13 (35.13%) of which were parasitized by ticks (Fig. 11), whereas Jacobson, the second most rural site, had 33 species of birds, of which 11 (33.33%) were parasitized by ticks (Fig. 12). Hoffler was a suburban site and had 42 species of birds, of which 13 (30.95%) were parasitized by ticks (Fig. 13). Both Paradise and Weyanoke were urban sites. Paradise had 31 species of birds, of which 2 (6.45%) were parasitized by ticks (Fig. 14), and Weyanoke, the most urban site, had 31 species of birds, of which zero (0.00%) were parasitized by ticks. The proportion of birds parasitized varied across sites relative to species richness (X=20.964, df=4, P<0.001; Fig. 13), and AIC predictions showed a negative relationship between proportion of birds with ticks and species richness (Fig. 8). However, because many of the birds that were most commonly caught at each site such as, Carolina Wrens, Northern Cardinals, and White-throated Sparrows, were parasitized only at sites where other bird species were also parasitized, further analyses were not pursued, as it was evident that ticks were not choosing different species of birds to parasitize based on how urban the environment was. (Figs. 15, 16, 17, 18).

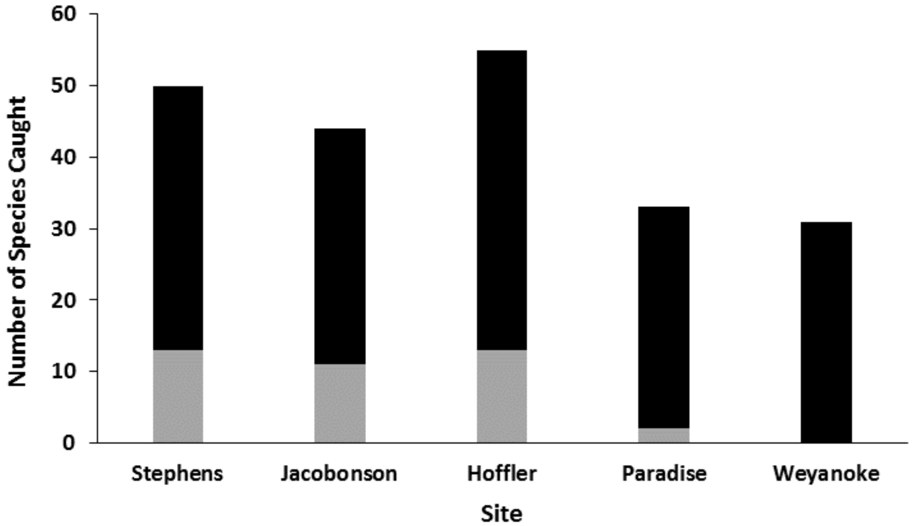

Figure 14. The number of species caught by site. The subset of species found parasitized by ticks is indicated in gray.

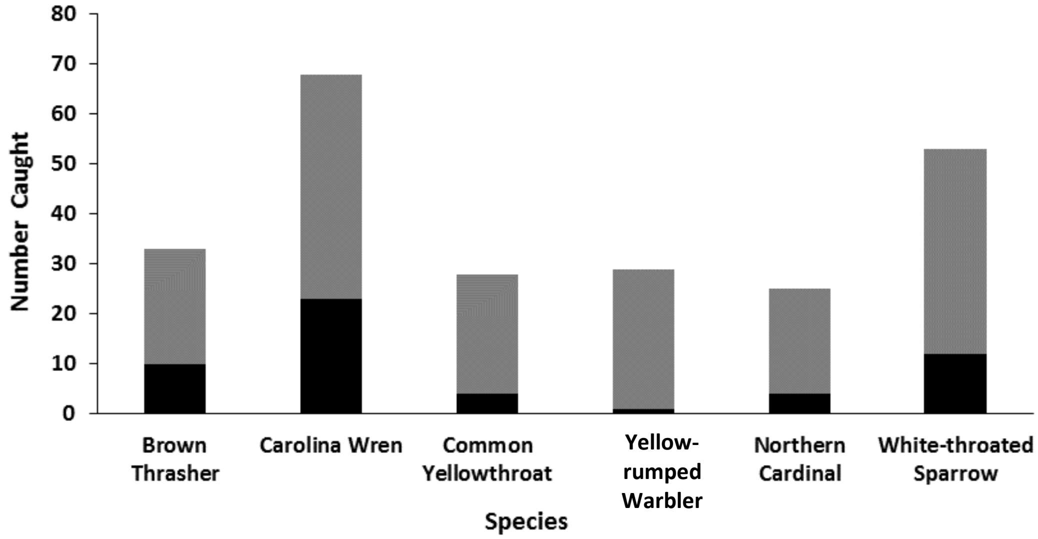

Figure 15. Stephens: Tick parasitism for bird species where ≥ 15 individuals were caught and at least 1 individual was parasitized by a tick. The subset of individuals found parasitized by ticks is indicated in black.

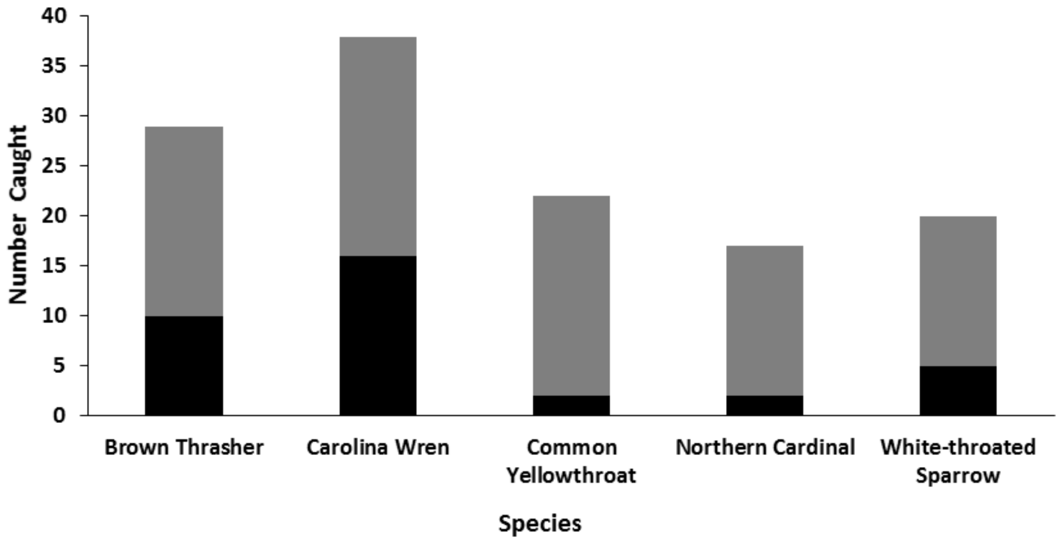

Figure 16. Jacobson: Bird species with ≥ 15 individauls caught and at least 1 individual with a tick. The subset of individuals found parasitized by ticks is indicated in black.

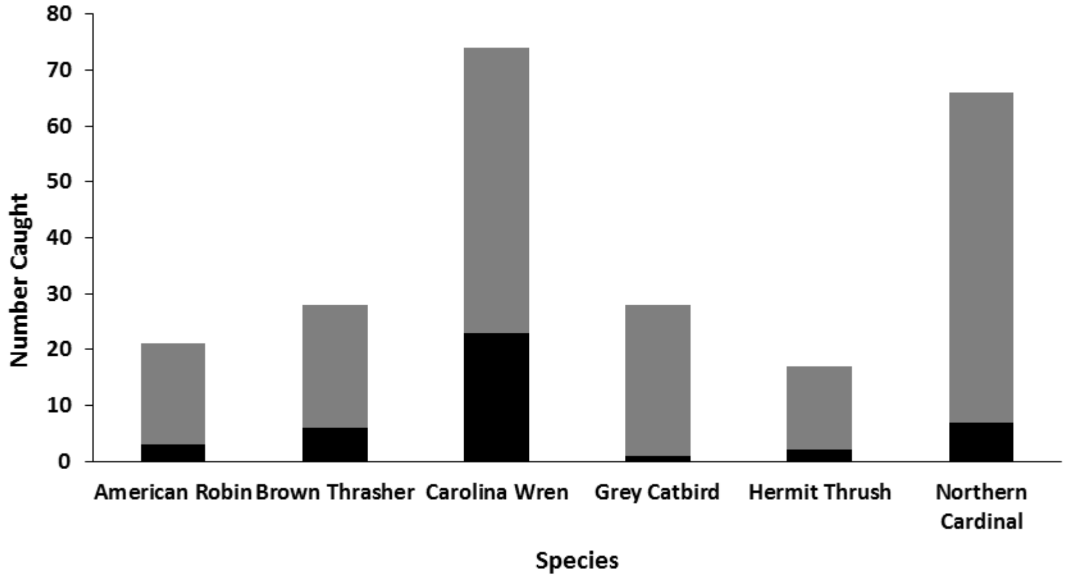

Figure 17. Hoffler: Bird species with ≥ 15 individauls caught and at least 1 individual with a tick. The subset of individuals found parasitized by ticks is indicated in black.

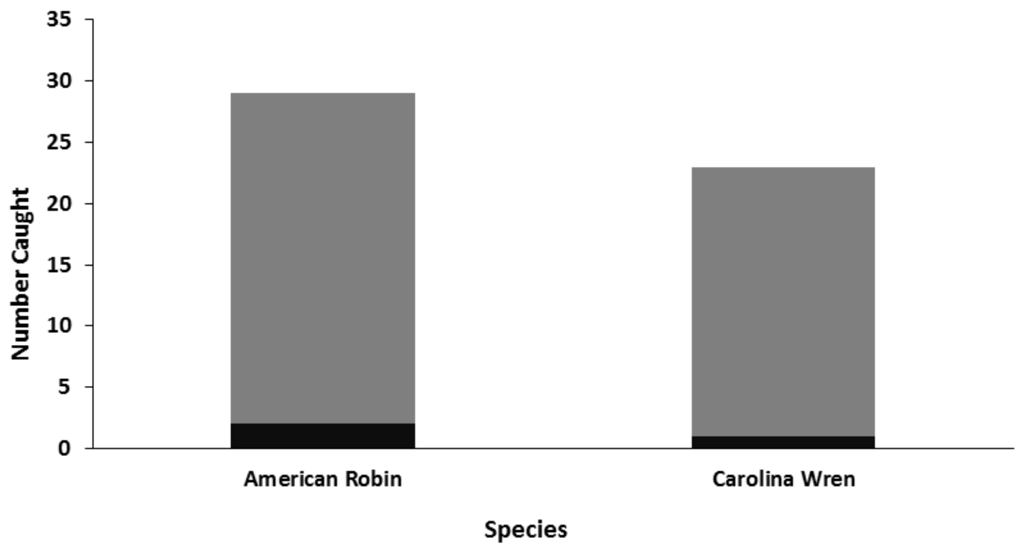

Figure 18. Paradise: Bird species with greater than or equal to 15 individauls caught and at least 1 individual with a tick. The subset of individuals found parasitized by ticks is indicated in black.

DISCUSSION

Because urbanization is increasingly relevant world-wide, and coastal southeastern Virginia is no exception, studying how urbanization affects wildlife in different ways is imperative to our understanding of how animals respond to factors that limit their habitat (De Silva and Marshall 2012). Increasing urbanization typically displaces wildlife and the ectoparasites associated with the wildlife (Bradley and Altizer 2006, Hunt et al. 2013, Schaefer and Gonzales 2013). Urbanization also decreases species diversity and may increase disease pathogen prevalence due to a reduction of pathogen-competent hosts in the area (Schmidt and Ostfeld 2000, Melles et al. 2003, Bradley and Altizer 2006, Swaddle and Carlos 2008, Pongsiri et al. 2009). Many bird species are negatively affected by urbanization as suitable habitat is lost (Philippe et al. 2002). Because ticks parasitize birds, and birds are affected by increasing levels of urbanization, it follows that urbanization should also affect ticks (Anderson and Magnarelli 1984). Although many studies have explored the relationship among birds, ticks, and urbanization (Hoch et al. 1971, Semtner et al. 1971, Maupin et al. 1991, Ostfeld et al. 1995, Peters 2009), this study is unique in that it was conducted year-round in a region along a migratory flyway, a migratory route to millions of birds each year (Hinshaw et al. 1985). This region, which provides temporary habitat for many migratory species, is experiencing urbanization at an alarming rate (Eggeman and Johnson 1989). Because of this, understanding how this increase in urbanization affects birds and their parasitic hosts is imperative.

IMPERVIOUS SURFACE HYPOTHESIS

Forty-four models were ranked using an information-theoretic approach to predict the site variable(s) that was/were the best predictors of tick parasitism. When including all permanent field sites, the best model included impervious surface cover at the 500 m buffer (Tables 5, 6). The parameter estimate for impervious surface at the 500 m buffer was negative, indicating that an increase in impervious surface cover reduces tick parasitism rates on birds (Figs. 8). A negative relationship between tick parasitism and impervious surface is not surprising (Table 9), as ticks are unable to survive on impervious surfaces (Hoch et al. 1971, Semtner et al. 1971). Because ticks typically require high moisture found in leaf litter, impervious surfaces do not provide suitable habitat for ticks (Hoch et al. 1971). The lower the impervious surface at 500 m, the higher the tick parasitism rates. Impervious surfaces do not provide good habitat for ticks and thus these areas of impervious habitat may be impeding the ability of ticks to colonize or disperse among urbanized habitat (Carreiro et al. 1999, Lu and Went 2006).

When comparing the ad-hoc sites to the permanent sites with respect to impervious surface cover at the 500 m buffer, I found that the majority of the ad-hoc sites matched the predictive models that were based on the five permanent sites, suggesting that the prediction plots show a trend across other sites (Fig. 8). The only impervious surface at 500 m outliers were Kiptopeke and Blackwater, which both exhibited a higher proportion of birds parasitized relative to percent impervious surface than expected. This finding may be an anomaly given that Kiptopeke was only sampled twice, both times in late August when larval tick masses, including

Table 9. Mean percent impervious surface by site calculated using ArcGIS 10.3 using 500, 1000, and 1500 m buffers. Proportion of birds with ticks presented using field data.

Site	**% Impervious**	**Proportion with Ticks**
Weyanoke	51.12076	0.000000
Paradise	25.32515	0.000247
Hoffler	12.28869	0.008146
Jacobson	7.195756	0.022459
Stephens	0.000000	0.014361
Kiptopeke	3.447595	0.224744
Hidden Cove	19.02563	0.034193
Suffolk	1.249742	0.041781
Virginia Zoo	41.36389	0.018302
York	1.530283	0.110345
Blackwater	0.133003	0.549199

rabbit ticks, are abundant, and Blackwater sampled three times, during the fall and early winter when larval tick masses are also abundant (Lindgren and Gustafson 2001).

The prediction for percent impervious surface cover was best at the 500 m buffer, likely because the 500 m buffer encompassed each site without encompassing much surrounding areas. The 100 m buffer did not encompass the entirety of every site and therefore likely does not as accurately describe cover types as the 500 m buffer. The 1000 m and 1500 m buffers were large and encompassed much land beyond the boundaries of each site. This habitat heterogeneity at larger buffer distances might explain why these two models did not have as much support. Since several of the sites were surrounded by either suburban or urban areas, ticks would be less likely to be found outside of the sites' boundaries.

Results regarding the best predictors of tick parasitism were very different when I eliminated Paradise and Weyanoke from these analyses. No ticks were collected from Weyanoke and only three were collected from Paradise over the course of two years, suggesting that very few ticks are found at these heavily urbanized sites. Using only Hoffler, Jacobson, and Stephens, season was the highest ranked model. Because both Weyanoke and Paradise had very high impervious surface percentages and also very few, if any, ticks present, these sites likely biased the models by suggesting percent impervious cover was more important in regards to predicting tick parasitism than it may actually be. When I looked at only the three permanent field sites that consistently had birds with ticks, there was much less effect of impervious surface on whether a tick was present or not. Additionally, season ranked as the best model, as the number of ticks I collected from birds varied based on season (Figs. 9, 10). It is interesting, however, that the relationship between winter and spring was the best predictor of parasitism within season, as I collected more ticks from birds during the fall than during the spring (Figs. 9, 10). I would have expected that the relationship between winter and fall would have yielded a stronger relationship, as birds were parasitized more frequently in the fall and the least in the winter. A possible explanation of this could related to the number and types of migratory birds that pass through Virginia during the spring versus fall migration. For example, if the spring migration yields more migratory birds stopping in Virginia that share tick habitat than the spring migration, it logically goes that more migratory birds would be parasitized in the spring than in the spring. Because very little is known about when different species of ticks are most active at their different life stages in coastal southeastern Virginia, this analysis suggests that season is important in predicting tick parasitism and demonstrates that additional study of these phenology-related questions is needed.

Following season as the top ranked model, the additive combination of season and species richness was also strongly supported as a predictor of tick parasitism. The model averaged proportion of birds with ticks decreased with increasing avian species richness (Fig. 11). Other studies (McKinney 2008, Nagendra et al. 2013, Aronson et al. 2014) have suggested that an increase in species richness decreases tick parasitism rates, and my study supports this claim. A potential explanation for this concerns the life histories of the various bird species. For example, an increase in bird species that rarely come in contact with ticks due to little overlap in habitat could cause this trend. Therefore, less commonly caught bird species likely are overrepresented while commonly caught species are underrepresented.

ENVIRONMENTAL CONSTRAINT HYPOTHESIS

The environmental constraint hypothesis posits that birds in urban areas are less likely to be parasitized by ticks than those found in rural areas. Urban areas lack suitable tick habitat due to higher impervious surface cover (Lu and Went 2006). Ticks require leaf litter and vegetation in order to survive, two components not typically found in highly urban areas (Carreiro et al. 1999). An increase in impervious surface, which positively corresponded with an increase in urbanization, predicted lower tick parasitism rates on birds than less urban sites.

This hypothesis was addressed using two approaches. The first limited analyses to three species of birds (Northern Cardinal, Carolina Wren, and White-throated Sparrow) and examined how these species were affected by ticks at each urbanization level. The three species were found at all sites in relatively high numbers, and all were parasitized by ticks at some point. They, therefore, were appropriate candidate species to address how urbanization affects tick parasitism rates (Fig. 8). Overall, the birds caught were more commonly parasitized by ticks as one crossed the urban gradient from rural to urban. These three species likely were commonly parasitized by ticks because they all spend time on or near the ground and therefore share habitat with ticks. Interestingly, while Northern Cardinals and Carolina Wrens are residents to Virginia and therefore were caught during all seasons, White-throated Sparrows are fall migrants. They, therefore, only spend winters in Virginia. Even though tick numbers were lower during the winter than during other seasons, White-throated Sparrows were still parasitized frequently by ticks. It could be that White-throated Sparrows spend more time on the ground than other species. Another potential explanation of why these three species were commonly parasitized is simply that they were abundant at all sites. This finding could, therefore, simply be an artifact of sampling; however, because these were the only three species of birds caught in high numbers across all sites, it is difficult to determine whether this pattern would hold for other species. Unfortunately, there were no other species caught in high enough numbers to test this premise.

All of these findings, however, support the environmental constraint hypothesis. Ticks are constrained by the environment, therefore, birds living in more rural sites are parasitized by ticks more commonly than those living in urban areas (Peters 2009). Rural habitats tend to provide adequate amounts of moisture (typically through leaf litter) that ticks need to survive (Knulle and Rudolph 1982), as opposed to more urban areas that tend to have less leaf litter due higher impervious surfaces and lower green cover (Carreiro et al. 1999).

The second approach examined only those species where at least ten individuals were caught among all sites, of which at least one individual was parasitized by a tick. Whether the species was caught at all sites or only one was irrelevant, as I was interested in solely addressing the effect of avian species on tick parasitism. This analysis again showed that birds were more commonly parasitized by ticks at rural sites than at urban sites. Birds at suburban sites were more commonly parasitized than those at urban sites, but no difference in tick parasitism was found between rural and suburban sites, suggesting that ticks are only sensitive to habitat up to a threshold. There is apparently not enough difference in impervious surface or vegetative cover between suburban and rural site to significantly affect tick parasitism rates. The birds most commonly caught at rural sites included: Carolina Wren, Common Yellowthroat, Chipping Sparrow (*Spizella passerina*), Brown Thrasher, White-throated Sparrow, Northern Cardinal, and Gray Catbird. The most common birds caught at suburban sites included: Carolina Wren, American Robin, Brown Thrasher, Gray Catbird, Yellow-rumped Warbler, Carolina Chickadee, and Northern Cardinal. This demonstrates, however, that the birds that were most commonly caught at rural sites were very similar to those caught at suburban sites.

Both of these analyses suggest that birds are more commonly parasitized by ticks at rural sites than at urban sites. Birds commonly caught at all permanent sites (including the urban ones) were only parasitized at the more rural sites, suggesting that there is an environmental constraint in urban areas that prevent ticks from living there. Therefore, if no ticks are living in the area, birds that live there will not be parasitized.

HOST CONSTRAINT HYPOTHESIS

The host constraint hypothesis posits that ticks show less avian-host preference in urban areas than in rural areas due to decreased avian species diversity. This decline in species richness associated with urban environments results in a constraint on hosts that would normally be available in more rural areas. Ticks found in urban areas would thus be forced to parasitize species they not normally encounter or prefer in rural areas.

The proportion of species parasitized varied across sites (Fig. 14). Species such as Carolina Wrens were caught with similar frequencies among sites; however, Carolina Wrens were parasitized by ticks at very different rates depending upon urbanization level of the site. Urban sites had far fewer Carolina Wrens parasitized by ticks than both suburban and rural sites. Even if there had been greater avian species diversity among urbanization levels, it is apparent that ticks are limited more by their environments than their hosts. Additionally, the model predicting that species richness affects tick parasitism suggests that an increase in avian diversity decreases the proportion of birds with ticks. This relationship is likely an artifact of the specific life histories of the additional avian species. The more species in an area, the more likely it is that some species do not spend any time on the ground in prime tick habitat.

This study shows how urbanization affects the relationship between birds and ticks. Understanding this relationship is imperative, albeit complicated, as birds tend to be more mobile than other tick hosts and therefore more likely to disperse ticks over long distances (Hasle 2013). This suggests that birds may play an important role in transporting ticks and tick-borne pathogens into novel areas, potentially increasing both tick and pathogen ranges (Philippe et al. 2002, Melles et al. 2003). During fall and spring migrations, this complication is amplified, as numerous migratory species of birds travel through Virginia on their way to breeding or wintering grounds (Hinshaw et al. 1985). Other common tick hosts, such as the white-tailed deer and the white-footed mouse cannot travel as far and as quickly as birds and do not share such extreme migratory tendencies (Scott et al. 2001).

Additionally, this study has implications for the public's perception of the effects of urbanization on wildlife-related policy-making and on public health. An increase in urbanization is leading to a decrease in the public's appreciation for nature (Theobald et al. 1997, Patterson et al. 2003, Sandry 2013). This is potentially dangerous to the welfare of wildlife, as policies are typically put in place based on public vote. If the public is unaware of the negative affects urbanization has on species diversity, they may vote for policies that do not protect wildlife (Theobald et al. 1997, Patterson et al. 2003). Public health also may be affected, as the consequent decrease in biodiversity in more urban areas may lead to an increase in the proportional abundance of reservoir-competent hosts for pathogens, a concept referred to as the dilution effect (Schmidt and Ostfeld 2000, Melles et al. 2003, Bradley and Altizer 2006, Swaddle and Carlos 2008, Pongsiri et al. 2009). Although it is unlikely that all bird hosts are competent reservoirs for various tick-borne diseases, the concept of an increase in disease pathogen presence caused by increased urbanization should bring the bird-tick relationship into a perspective that relates to the public. Ecologists also should be interested in this topic, as little is known regarding avian host-competence, suggesting that many questions are left unanswered and waiting to be researched.

This study is also the first of its kind, to my knowledge, that addresses how urbanization affects the seasonal relationships among avian hosts and ticks year-round. Other studies were limited to the fall and spring when birds are migrating and more likely to be caught in higher numbers (Olsen et al. 1995, Bjoersdorff et al. 2001, Reed et al. 2003, Desante et al. 2008). While these studies provide valuable information on how urbanization affects the relationship between birds and ticks, they are limiting in that they only address half of the year. This study used more rigorous methodology by sampling year-round in order to determine what relationships, if any, there are between birds and ticks during previously ignored parts of year. The data showed that ticks are attaching to avian hosts year-round and therefore are likely parasitizing other animals, including humans, year-round. Because I found ticks during the winter and summer, the two non-migratory seasons, it is imperative that ecologists interested in tick dynamics address their questions during every season. In particular, it is surprising that summer has often been ignored, as ticks appear to be present in relatively high numbers during this season, as opposed to the winter when tick abundance is lower (but not zero). Results from this study support that ticks actively seek hosts year-round and therefore, tick related studies should not be limited to any particular season.

Overall, this study showed a relationship among urbanization, birds, and ticks. In general, birds in more urban areas are less likely to be parasitized by ticks than birds in rural areas. Urban areas have high impervious surface cover, effectively limiting ticks' ability to survive. Other biotic factors, such as vegetation cover, also play a role in tick dynamics, as do abiotic factors such as season. Clearly, the relationship between birds and ticks is highly complex and dependent upon several environmental conditions.

CHAPTER III

TICKS PARASITIZING BIRDS IN COASTAL SOUTHEASTERN VIRGINIA

INTRODUCTION

Phenology is the study of the annual life cycles of organisms and how these cycles are influenced by seasonal, annual, and temporal factors (Edwards and Richardson 2004). In more recent years, the effects of global climate change on plant and animal phenologies have become increasingly studied and discussed (Stevenson and Bryant 2000). Changes in climatic patterns and temperature can have drastic effects on many species, particularly those that time their breeding around temporal conditions (Crick and Sparks 1999, Stevenson and Bryant 2000). Because life history traits are critical to fitness, understanding the phenologies of species and the factors that affect them is of the utmost importance. Climate change, however, is only one example of areas pertinent to the study of phenology. Understanding the phenology of an organism is imperative to fully comprehend that organism's life history and behavior and is important to addressing its relationships with other organisms.

AVIAN PHENOLOGY

There are an estimated 10000 species of birds worldwide, 2098 of which are native to North America (American Ornithologists' Union 2015). Hundreds of species of birds use migratory flyways in North America each year during their fall and spring migrations (Eggeman and Johnson 1989). Understanding the phenology and movement patterns of these birds is critical to conservation efforts. Because avian taxa vary widely in their life histories, morphology, and behavior, they have varying habitat requirements, food preferences, and life-history traits that can affect their relationships with other taxa (Saether and Bakke 2000). Therefore, increased study of the many species, especially those of conservation concern, that travel through North America is mandated.

AVIAN FORAGING AND NESTING GUILDS

A keystone of ecological research is understanding variation in behavior and occurrence of both flora and fauna (Holway and Suarez 1999). Often these patterns are driven by differences in the environment due to systemic and stochastic environmental heterogeneity (Dorazio and Connor 2013). Because there are so many species of birds in North America, let alone the world, researchers often group species into categories in order to simplify their analyses. Groups of species that use the same resources in similar ways are often referred to as members of the same guild (Adams 1985). The concept of a guild was initially introduced as a way of understanding community structure (Simberloff and Dayan 1991). The species within a given community interact frequently due to shared habitat or similar feeding preferences are often compete for shared resources (Dorazio and Connor 2013). Because of this intra-guild competition, more diverse habitats often support higher species richness, as competition may be reduced (Pearman 2002).

Avian ecologists often focus on foraging and nesting guilds, as foraging and nesting habits of birds provide valuable information on where individual species spend their time, why they behave in certain ways, and during what times of year do these foraging and nesting behaviors differ. Foraging guilds, as the name suggests, comprise species that forage in a particular manner or on a particular resource.

Examples of commonly used avian foraging guilds include, but are not limited to: ground, shrub, canopy, and aerial foragers (Ehrlich et al. 1988, DeGraaf 1991). Nesting guilds often describe the habitat or niche where birds make their nests. Common nesting guilds include, but are not limited to: hole, ground, shrub, low canopy, mid-canopy, cavity, and high canopy nesters (Ehrlich et al. 1988, Park and Lee 2000).

MIGRANT VS. RESIDENT BIRD LIFE HISTORIES

Avian taxa are often grouped into resident or migratory taxa (Sol et al. 2010). Migratory status affects where birds live at different times of year, where they raise their young, and what their energetic requirements are; because of this, migratory status plays a huge role in birds' lives. Resident taxa tend to remain in the same geographic region year-round, whereas migratory birds travel to different regions throughout the year (Ahola et al. 2007). Resident birds, therefore, do not have the same energetic requirements during the same period that migratory species are moving and arguably are more generalist in their survival requirements as they are able to remain in one area for the duration of the year (Odum et al. 1961). Migratory species typically move among regions because resources are limited at nesting or wintering sites and would not sustain these species year-round. Resident birds, however, are able to successfully utilize the resources in a single area year-round (Boyle 2006).

In North America, there are two major migration periods, one in fall and one in spring (Stanley et al. 2012). Many North American birds migrate south in the fall in order to spend their winters in warmer climates and then return north in spring to breed (Rappole et al. 2000). Southern hemisphere birds typically show the reverse trend (Dingle 2008). Some taxa can be both resident and migratory depending upon where they occur within the species' range. American Robins, for example, are migratory in Canada and Mexico but can be either resident or migratory in most of the continental United States (Pyle 2008). Interestingly, some of these populations co-occur during winter (Pyle 2008, Cornell Lab of Ornithology 2015).

Because migration is an energetically expensive task (Moore and Yong 1991), it is imperative to migratory birds' migration success that they gain adequate fat during their pre-fatting migration period in order to survive during their migrations (Klaassen et al. 2013); therefore, birds preparing for migration forage heavily before leaving for their migrations (Metcalfe and Furness 1984). Once fat stores are gained pre-migration, migratory birds in North and South America often travel very long distances to reach their breeding or wintering grounds (Alerstam 2001). Throughout this migration period, migratory birds spend more time foraging than most resident birds in order to regain fat stores (Odum et al. 1961). Birds that are mid-migration often make many stops along their migration routes to refuel (Mehlman et al. 2005). Some species stop every day to refuel, whereas others may only stop once in a couple of weeks (Schaub et al. 2001, Erni et al. 2002, Delinger et al. 2006). Species that stop every day, in particular, must forage quickly and efficiently in order to continue their journey (Gordo 2007). Where birds stop throughout their migration is variable as well. For example, some studies have found that juvenile birds arrive at stop-over habitat and final destinations later than adults and often stop closer to the coast than adults (Koko 1999). Understanding the migratory tendencies of birds can help elucidate the timing and frequency of foraging habits and the repercussions of various foraging styles (Schaub et al. 2001).

AVIAN AGE AND SEX

Both bird sex and age can affect behavior, and these behavioral differences are often most pronounced during the breeding season (Itoh and Ishii 1990, Anderson et al. 2004). Foraging habits and territorial behavior in particular vary between the sexes during the breeding season as birds prepare to feed and defend their young (Holmes et al. 1979, Eckhardt 1979, Holmes 1986). Many studies argue that male birds spend more time foraging and defending their territories during the breeding season than females (Orians 1969, Matysiokova and Remes 2014), as females often spend more time incubating eggs and being vigilant to vulnerable fledglings (Filliater and Breitwisch 1997). Sex-dependent behavior and preferences, however, can vary during non-breeding times as well, though the differences during non-breeding times are likely less obvious and studied (Lynch et al. 1985).

Age affects behavior in birds as well (Anderson et al. 2004). Often, while animals are young, their foraging endeavors do not result in the capture of food; however, these experiences enable young animals to learn to sustain themselves (Thornton and Raihani 2008). Because adult birds typically must teach their young how to forage and find food for themselves (Caro and Hauser 1992, Galef and Laland 2005), young birds often rely on their parents for food during this learning period (Caro and Hauser 1992). As fledglings grow, they must learn to scan for predators and search for food in order to survive (Sullivan 1988). Adults become less vigilant in regards for caring for and looking after their young as their young age, thus young birds must adjust their behaviors as they mature (Yasukawa et al. 1992).

TICKS

Ticks are arachnid ectoparasites that feed on vertebrate blood and are categorized into three major families: Argasidae (soft-bodied ticks), Ixodidae (hard-bodied ticks), and Nuttalliellidae (only found in Africa; Nelson et al. 1975, Sonenshine 1979, Anderson 2002, Chanie et al. 2010, Nadolny et al. 2011, Wright et al. 2011,). There are over 840 species of ticks in the world (Anderson 2002), though common to North America are rabbit ticks (*Haemaphysalis* spp.), *Amblyomma* spp., *Dermacentor* spp., and *Ixodes* spp., all of which are of the hard-bodied variety. Hard-bodied ticks feed for several days and up to two weeks until fully engorged, whereas soft-bodied ticks typically finish feeding within a few hours of attachment (Lawrie et al. 1999, Anderson 2002, Anderson and Magnarelli 2008).

Tick species vary in behavioral patterns and preferences (Randolph and Storey 1999), particularly with respect to locating hosts (Ginsberg and Ewing 1989). Ixodid ticks live on or near the ground, only tending to climb a maximum of a meter off the ground in order to locate hosts (Semtner et al. 1971, Carroll et al. 1998). Different species of ticks have varying host-finding strategies. Generally, ticks are described as either ambush hunters or questers (Carroll et al. 1995, Goddard 2013). Ambush hunters climb vegetation where they likely will encounter a host, whereas questers sense a host approaching, climb onto vegetation, and consequently grasp hosts as they walk by (Carroll et al. 1995). Most ticks in the United States are considered ambush hunters; however, *A. americanum* and *A. maculatum* are both considered to be questers (Goddard 2013). Ticks attach to their hosts' outer epidermis and insert a feeding tube, called a hypostome, into the skin in order to feed (Endo 1978). Many tick species secrete a cement-like substance in order to remain attached to their hosts for the extended period of time it takes for them to feed to repletion (Bishop et al. 2002).

In addition to having different strategies for locating hosts, ticks also vary in their host preferences (Cumming 1998, Christe et al. 2007). Many tick species are commonly found on large mammals (Anderson et al. 1983, Magnarelli et al. 1995). In the eastern United States, mammals, such as white-tailed deer, are considered to be the most common hosts for ticks (Bloemer et al. 1988, CDC 2015). Ticks, however, also parasitize avian, reptilian, and amphibian hosts (Sonenshine and Stout 1970, Anderson et al. 1986, Poupon et al. 2006), though they tend to have smaller tick burdens when compared to mammals (Giery and Ostefeld 2007). Birds, in particular, that forage and nest on the ground are susceptible to tick parasitism. They may experience smaller tick burdens than mammals because they are not limited to spending time on the ground as many mammalian counterparts are (Holmes and Robinson 1988, Antos et al. 2008, Rondini et al. 2008).

TICK AGE

The majority of Ixodid ticks have four life stages: egg, larva, nymph, and adult (Gardiner and Gettinby 1981, Spach et al. 1993); however, because eggs are not parasitic, they are generally not considered when examining the effect of age (Hitchcock 1955). Larval ticks are easily distinguished from other life stages in that they only have six legs, whereas nymphs and adults have eight (Anderson and

Magnarelli 2008). Larval ticks are very small and need a relatively small blood meal to survive (Ribeiro et al. 2012). Once larval ticks feed, they enter a diapause and eventually molt into their nymphal stage. Nymphs go through a very similar cycle as larvae in that they feed, enter diapause, and then molt to become adults (Oberchain and Galun 1982, Grimm et al. 2003). Once ticks become adults, females typically feed once before mating and then lay eggs. Most adult males do not feed to repletion. They solely mate and die (Sonenshine 2006).

Ticks in different life stages often have variable host preferences as well (Semtner and Hair 1973a,b). Adult ticks prefer larger hosts, whereas larval and nymphal ticks are more indiscriminate in their host choice based on size (James and Oliver 1990, Ribeiro et al. 2012). This relationship between host and tick sizes likely stems from the fact that larger ticks prefer larger hosts that can more easily and quickly supply necessary amounts of blood (Semtner and Hair 1973a,b).

RABBIT TICKS

Rabbit ticks (*Haemaphysalis leporispalustris*) are common parasites of rabbits, such as eastern cottontails (*Sylvilagus floridanus*; Camin 1978) and are commonly found in forested habitat with high shrub cover (Mankin and Warner 1999; Casher et al. 2002). Eastern cottontails also are well adapted to early-successional habitats and therefore could introduce rabbit ticks into previously uninhabited areas (Mankin and Warner 1999). Larval rabbit ticks typically hatch from eggs that are deposited on the ground following an engorged adult female detaching from a rabbit (Gamin and Drenner 1978). Although rabbit ticks' name suggests they feed solely on rabbits, larval and nymphal rabbit ticks will parasitize birds as well, whereas adult rabbit ticks are host-specific to rabbits (Camin 1978). This species of tick, therefore, must remain in areas that are very close to rabbit habitat in order to survive into adulthood and then reproduce; therefore juvenile rabbit ticks found on migratory birds are likely to die because they drop-off their hosts in areas not inhabited by rabbits (Gamin and Drenner 1978).

Ground foraging and nesting birds often serve as suitable hosts to larval and nymphal rabbit ticks (Hoogstraal et al. 1970, Gamin and Drenner 1978, Kinsey et al. 2000, Ogden et al. 2008). Because larval rabbit ticks are highly sensitive to light and moisture, they climb vegetation in order to escape saturated ground; however, if they do not successfully find a host, within a few hours they dry out and must return to the ground to prevent desiccation (Chi-Yen et al. 1973, Gamin and Drenner 1978). Generally, rabbit ticks prefer to utilize curved vegetation that is close to the ground as their hunting posts, making rabbits and ground-dwelling and ground foraging birds their preferred hosts (Gamin and Drenner 1978).

Rabbit ticks are less sensitive to environmental changes than many other species of tick and therefore have been documented parasitizing hosts year-round (Kollars and Oliver 2003). This is importance to humans because rabbit ticks are known carriers of tularemia, a zoonotic bacterial disease that causes symptoms such as ulcers and high fever in humans (Shah and Sunil 2013). Tularemia also negatively affects its wildlife hosts causes chronic infection in some hosts and death in others. Additionally, tularemia is capable of surviving within its tick host throughout diapause and therefore can remain in its host into future life stages (Bequaert 1945).

IXODES, DERMACENTOR, AND AMBLYOMMA SPECIES OF TICKS

Ticks of the *Ixodes* genus typically have legs that are black and are identifiable from other genera of ticks by the presence of an anal groove (Arthur 1956, Elston 2010). As there are many species with the *Ixodes* genus, behaviors and host preferences can vary widely depending on the species (Keirans and Clifford 1978). However, many members of the *Ixodes* genus are classified as questers rather than ambush hunters and have been reported feeding on mammals, birds, and amphibians (Keirans and Clifford 1978, Carroll et al. 1998, Kelman 2014). Others, such as *Ixodes scapularis*, are considered to be ambush hunters (Sonenshine 1993). They often choose where they will quest by sensing the kairomones and carbon dioxide emissions of potential hosts (Carroll et al. 1998, Carr et al. 2013, Kelman 2014).

Ticks of the *Dermacentor* and *Amblyomma* genera have legs that are tinged brown and lack an anal groove (Elston 2010). As with ticks of the *Ixodes* genus, there are numerous species within these two genera, so behavior and host preferences vary. Some species, such as *A. americanum*, actively pursue their prey (Sonenshine 1985, Goddard 2013); others, such as *D. variablis*, are ambush hunters (Sonenshine 1993). Species of tick within all three of these genera show sensitivity to kairomones and carbon dioxide and use these two factors to aide them in locating hosts (Carr et al. 2013).

SEASONALITY AND WEATHER IN RELATION TO TICKS

Seasonality, which affects temperature, rainfall, resources, and humidity, affects the relationship between parasites and their hosts (Altizer et al. 2006). Because

Ixodid ticks go long periods of time between meals, and therefore long periods of time without access to water, which they extract from their hosts' blood, ticks rely heavily on their environment to remain moist (Guerra et al. 2002).

Desiccation is the most common cause of tick-death, further supporting the importance of humidity and moisture in the environment (Knulle and Rudolph 1982). When Ixodid ticks feed, they return the water that is found in their hosts' blood back into their hosts (Seuer et al. 1995). This enables them to ingest more of the nutrient-rich components of blood, rather than filling-up on energy-deficient water (Knulle and Rudolph 1982). This also contributes to the process of pathogen transfer between parasite and host (Randolph et al. 1996).

While ticks that are feeding must release water, non-feeding ticks must conserve water and survive for months without ingesting water from their hosts' blood. Therefore, ticks avoid dehydration and ultimate desiccation by having specialized physiology to reduce water loss (Lees 1946, Browning 1954, Knulle and Rudolph 1982). Their exoskeletons are covered with waterproof waxy lipids that prevent water loss, and they are able to replace water loss by absorbing water from the atmosphere. These adaptations help ticks maintain homeostasis in order to prevent death by desiccation (Knulle and Rudolph 1982).

While much is known about how ticks feed, very little is known about when particular tick species and their three parasitic life stages are active. Tick occurrence is generally thought to be related to outside temperature. Ticks tend to be less active during cold weather, as they are prevented from finding hosts when they reach their activity threshold temperature (Clark 1995, Perret et al. 2000). The temperature at which ticks cannot successfully quest for hosts is positively correlated with body size, meaning smaller ticks reach this threshold sooner than nymphal and adult ticks (Clark 1995). Thus, larval and nymphal ticks likely are less active during cooler times of year than adults (Clark 1995, Perret et al. 2000).

Humidity also plays a role in tick occurrence (Altizer et al. 2006). Because hard-bodied Ixodid ticks often die from desiccation, living in an environment that has high humidity is imperative to their survival (Heath 1979). Therefore, the activity levels and survival of many tick species is related to relative humidity levels (Berger et al. 2014). Critical humidity levels can vary slightly between species. For example, *A. maculatum* requires higher humidity in it environment to prevent desiccation from internal water loss than *A. americanum* (Hair et al. 1975). Higher relative humidity also correlates with increased oviposition and reproductive fitness (Arijo and Qaimkhani 2014). Understanding the climatic and season-specific preferences of different species of ticks in different life stages can elucidate the enigmatic behavioral patterns of these animals.

RELATIONSHIPS BETWEEN BIRDS AND TICKS

The relationship between ticks and their avian hosts is strongly influenced by phenology of both host and parasite (Pegram et al. 1986). Because birds are hosts to ticks (Fig. 15), understanding how and why ticks choose their avian hosts is paramount to comprehending the relationship between host and parasite (Battaly et

Figure 19. Carolina Wren with 57 larval ticks caught at Hoffler Creek Wildlife Preserve on November 6, 2012.

al. 1987). In order to understand this relationship, addressing both avian and tick phenologies and how they intertwine is necessary.

Ticks in their larval and nymphal life stages are common parasites of avian taxa (Anderson et al. 1990, Scharf 2004). As larvae or nymphs, these life stages are typically smaller than adults and therefore require smaller blood meals that can readily be provided by smaller animals. Adult ticks rarely are found on birds, as they prefer to parasitize larger animals (Wilson et al. 1985).

In order to comprehend host-parasite interactions, understanding the foraging habits of host species is crucial. The likelihood of birds being parasitized by ticks and the number of ticks found on each bird can be related to the propensity for the bird host to forage on the ground (Stafford et al. 1995, Eisen et al. 2004). Similarly, host nesting behavior likely affects the frequency of parasitic interactions. Birds that nest on the ground are more likely to be parasitized by ticks than those that nest in the canopy or in cavities (Stafford et al. 1995). Birds that spend more time on or near the ground, whether foraging or nesting, share their environments with ticks (Hoch et al. 1971, Alder et al. 1992, Peters 2009). Therefore, interactions between bird hosts and tick parasites are common (Rand et al. 1998).

The complex interaction between seasonality and bird-tick life histories is an important research area. For example, fall and spring migrations often correspond with when ticks are most active (see above, "*Seasonality and Weather in Relation to Ticks*"), further increasing potential parasitism (Wilson et al. 1984). Because of this relationship between bird migration and tick activity, previous studies have focused on bird-tick interactions during fall and spring migrations (Heffernan et al. 2014).

Bird age and sex also likely affect the propensity for an individual to be parasitized by ticks (Hamilton and Zuk 1982, Clayton and Moore 1997, Gregoire et al. 2002). There is no consensus on whether younger juvenile birds versus adult birds have a greater probability of parasitism. Some studies indicate that juvenile birds are more likely to be parasitized, especially by ticks that are commonly found in nests (Hamer et al. 2012a). Juvenile birds spend time in their nests as nestlings and then substantial amounts of time on or near the ground as fledglings, potentially increasing their chances of encountering foraging ticks (Woodward 1983, Soler 1994). Other studies have found that adult birds are burdened by ticks more often than juveniles, as they spend more time foraging for food in order to feed themselves and their young (Gregoire et al. 2002). Others still have found no difference in tick parasitism rates in relation to bird age (Heylen and Matthysen 2008).

Whether male or female birds are more commonly parasitized by ticks is another contested concept. Because foraging habits during the breeding season often vary between males and females, tick parasitism rates on male and female ground foraging birds likely varies (Holmes et al. 1979, Eckhardt 1979, Holmes 1986). Some argue that because males spend more time foraging and defending territories during the breeding season, that ground foraging males exhibit higher tick abundances (Orians 1969, Matysiokova and Remes 2014). However, many female ground foraging and ground nesting passerines spend more time in their nests, which could increase their likelihood of being parasitized (Jones 2008). Additionally, Holmes (1986) found that the females of several species of warblers, vireos, and flycatchers forage closer to the ground than the males of these species. This would suggest that females of these species may be more heavily parasitized by ticks over their male partners during the breeding season (Holmes 1986). Others studies have found no difference in tick parasitism rates relative to sex (Gregoire 2002, Scharf 2004).

Tick burdens and parasitism rates vary by host species (McDade and Newhouse 1986). Although birds may have smaller tick burdens than various mammal species (Giery and Ostefeld 2007), birds differ from most mammals in that they are homoeothermic vertebrates that often have very large home ranges and can travel long distances in a very short timeframe (Scott et al. 2001, Peters 2009). Marine mammals and many insect species, for example, also travel great distances (Williams 1958, Kennedy 1961, Smith et al. 1999, Mate and Lagerquist 1999); however, marine mammals do not live in environments that support ticks, as ticks can only live short term when inundated with water (Kahl and Alidousti 1997), and insects are not known hosts for ticks (Van Buskirk and Ostfeld 1995). Other terrestrial animals with long migrations, such as the wildebeest (*Connochaetes spp.*), have an innate resistance to ticks and do not support high tick burdens (Fyumagwa et al. 2007). Bats, in the order Chiroptera, an example of a flying mammal, are known hosts to ticks, particularly the host specific bat tick, *Carios Ornithodoros kelleyi* (Lausen 2005; Loftis et al. 2005, Sevcik et al. 2010); however, bats have been found to be mostly accidental hosts to most Ixodid ticks (Walter and Kock 1985).

HYPOTHESES

The vagility of birds enables them to transfer ticks and tick-borne pathogens across more substantial distances than mammals (Peters 2009). Their ability to travel could bring new species of ticks and new pathogens into previously uninfected areas or even across varying habitat types (Battaly et al. 1987, Scott et al. 2001, Peters 2009). Previous studies looking at bird-tick relationships have been biased towards migration periods, presumably because (1) birds may be more active during this time and may be more likely to be captured, (2) banding stations are focused on migrants (Desante et al. 2008), and (3) ticks often are more active during the fall and spring seasons (Anderson and Magnarelli 1984, Brunner and Ostfeld 2008, Peters 2009). These studies, therefore, have been biased with respect to time of year. The following study involves a year-round approach to understanding bird-tick relationships within the context of the effects of urbanization (see Chapter II) in order to reduce time of year biases and to make predictions about how both bird and tick phenologies affect the relationship between birds and ticks.

In this study, I addressed eight hypotheses that relate to avian and tick phenologies:

1. G*round Foraging Hypothesis*: Ticks are more likely to parasitize birds that are classified as ground foragers. Because ticks spend their lives very close to the ground, their ability to parasitize birds that forage above the ground is limited (Rand et al. 1998); therefore, species that stop frequently and spend time foraging close to the ground are highly susceptible to being parasitized by ticks (Peters 2009).

2. Ground Nesting Hypothesis**:** Ticks are more likely to parasitize ground nesting birds. Because ticks spend their lives very close to the ground, their ability to parasitize birds that nest above the ground during the avian breeding season is limited (Semtner et al. 1971, Carroll et al. 1995); thus, birds that forage close to or on the ground should exhibit higher tick prevalence rates than those that nest further from the ground (Stafford et al. 1995).

3. Migratory Bird Hypothesis**:** Ground foraging migratory birds that travel during fall and spring migrations are more likely to be parasitized by ticks than ground foraging resident birds. Migratory birds have higher energy requirements than resident birds (Odum et al. 1961); therefore, ground foraging migratory birds must prepare for and refuel themselves to successfully complete such an energetically expensive venture. Thus, ground foraging migratory species spend more time on or near the ground during these period. This puts them at higher risk for tick parasitism than resident ground foraging birds (Wilson et al. 1984, Moore and Yong 1991).

4. Dirty Juvenile Hypothesis**:** Juvenile birds spend more time near the ground during their fledgling stage and are therefore more likely to be parasitized by ticks than adult birds. Juvenile birds spend a majority of time in nests directly following hatching, foraging on the ground and learning to fly (Woodward 1983, Soler 1994). This increased time on the ground increases the potential contact time within tick habitat and therefore increases their likelihood of being parasitized by ticks (Semtner et al. 1971).

5. Dirty Male Hypothesis**:** Male birds are more likely to be parasitized by ticks than females during the breeding season. Males, particularly during the breeding season are more aggressive and often spend more time foraging than females (Hau et al. 2000). If the males are ground foragers or defend territories that are on or near the ground, they may come in more frequent contact with ticks than their female partners (Orians 1969, Matysiokova and Remes 2014).

6. *Bird Weight Hypothesis:* Heavier birds are more commonly parasitized than lighter birds. These larger birds emit more carbon dioxide than smaller birds, which attract ticks and also have greater body masses and surface areas, which make them more likely to encounter ticks that lighter birds with smaller masses (Maturano et al. 2015).

7. Tick Stage Hypothesis**:** Juvenile larval ticks more commonly parasitize birds than do nymphal or adult ticks (Weisbrod and Johnson 1989). Adult ticks prefer larger hosts, as they require larger quantities of blood (James and Oliver 1990, Ribeiro et al. 2012). This results in larval ticks parasitizing birds more frequently than either nymphal or adult ticks.

8. Tick Seasonality Hypothesis: The phenology of ticks results in life stages being present at different times of year. It is believed that larval and nymphal ticks are more active in summer and fall when humidity is high, which reduces their risk of desiccation (Berger et al. 2014); however, little data have been collected previously to confirm this pattern with any certainty. Therefore, birds are more likely to be parasitized by ticks during summer and fall months than during other times of the year because ticks are more active and abundant during these times.

METHODS

This study took place at five sites in coastal southeastern Virginia, along a major migratory flyway in North America (Eggeman and Johnson 1989). The sites were located in the city of Norfolk, the city of Portsmouth, and the city of Chesapeake. Within this region, there are 13 documented species of ticks (Table 7). Which of these species are known to parasitize birds, when, and at what frequency are unknown.

SITES

For information regarding the sites sampled for this study, refer to Chapter II.

BIRD AND TICK SAMPLING

For detailed information on bird and tick sampling methods, refer to Chapter II. All tick samples were separated into taxonomic categories based on morphological characters observed using an Olympus SZ61 dissecting microscope (40 x magnification, manufacture, place of manufacture), particularly for nymph and adult life stages. Larvae identification was confirmed molecularly using PCR (de la Fuente et al. 2011, Nadolny et al. 2011, Wright et al. 2014). Within this study's region of southeastern Virginia, 14 tick species have been reported (Table 1).

STATISTICAL METHODS

Categorical variables used in analyses included: month, year, season, site, bird species, bird age, bird sex, migrant status, migration period, species richness, nesting guild, foraging guild, species, and tick life stage. Season was defined as:

winter (December – February), spring (March – May), summer (June – August), or fall (September – November). Bird age and sex were categorized as discussed above. Migration status was either resident or migratory, and migration period was either fall or spring (Pyle 2008). Species that could be either migratory or resident, such as American Robins, were labeled as resident for the purposes of this study. Tick life stage was categorized as larva, nymph, or adult. Site size and the species richness at each site during each season were also recorded.

In order to tease apart complex life history phenomena, I grouped avian species into both foraging and nesting guilds based on the classification used by Ehrlich et al. (1988) and the Cornell Lab of Ornithology (2015). A guild was defined as a group of species that use similar resources in similar ways (Adams 1985, Simberloff and Dayan 1991). For the purposes of this study, foraging guilds were divided into three categories: (1) mainly ground foragers, (2) mainly foliage foragers, and (3) mainly aerial foragers. Nesting guilds also were divided into three categories: (1) ground nesters, (2) shrub nesters, and (3) canopy nesters (Table 10).

For all phenology analyses, data from all years were combined. All phenology statistical analyses were limited to sites where greater than five ticks were collected off birds throughout the entire duration of the study. Because no ticks were collected from Weyanoke, and only three ticks were collected from Paradise, these two sites were eliminated from all analyses. Species of birds that had no individuals parasitized by at least one tick were also eliminated from all analyses.

When conducting analyses pertaining to foraging and nesting guilds, I excluded any season where less than 15 ticks were collected at each of the three sites used in these analyses. Therefore, the winter season (December - February) was omitted. In the Eastern United States, fall migration typically occurs from August to October, whereas the spring migration occurs from March to May (Pyle 2008). Thus, analyses pertaining to migration were also restricted to months when birds were migrating (Table 8); therefore, January, February, June, July, November, and December were omitted. Analyses examining bird age and bird sex were restricted to seasons where greater than 15 ticks were collected as well, again eliminating the winter season. All analyses, except for the one pertaining to season, excluded the winter season. The response variable for all analyses was binary (parasitized by a tick yes/no); therefore, I was not concerned about overinflation of zeroes, as binary data cannot result in this type of overinflation (Ridout et al. 1998).

Logistic regression in SPSS was used for all analyses because data were not normally distributed (IBM SPSS Statistics 21.0, Chicago, IL). The assumptions for logistic regression included: (1) dependent variable is dichotomous, (2) at least one independent variable must be either continuous or categorical, (3) observations are independent of one another, and (4) there is a relatively linear relationship between continuous independent variables and dependent variables (Menard 2002). Data were checked to ensure that they met the assumptions for logistic regression. The assumption regarding observations are independent was not fully met, as recaptured birds were used in analyses. I used recaptures, as all ticks were removed from each individual before release and therefore if a bird was recaptured, it had an equal opportunity to be parasitized or not. Additionally, all recaptures occurred at least two weeks apart, enough time for any unfound ticks to fall-off before recapture.

RESULTS

For Hoffler, Jacobson, and Stephens, the three permanent field sites used for these analyses, a total of 822 captures of birds representing 74 species occurred in 4576.67 net hours over 154 netting sessions for an overall netting success rate of 18.0 captures per 100 net hr. Hoffler and Stephens were both sampled from August 2012 to August 2014. Jacobson was added later as a sampling site and was sampled from June 2013 to August 2014.

Recaptured birds comprised 139 (16.9%) of captures, though only 29 (3.8%) were parasitized by ticks. Of the recaptured birds parasitized by ticks, 25 (86.2%) were parasitized more than once. Only five of the parasitized recaptured birds were migratory (four White-throated Sparrows and one Swamp Sparrow). Birds were most commonly recaptured at Weyanoke, an urban site with no ticks. The five most abundant species captured were: Carolina Wren (*n=118*, 14.3%), Northern Cardinal (*n*=95, 11.5%), White-throated Sparrow (*n=73*, 8.8%), Yellow-rumped Warbler (*n=66*, 8.0%), and Brown Thrasher (*n=64*, 7.8%).

Of 799 ticks collected, only 0.4% were adults. All three of these adults were rabbit ticks found on a juvenile male Eastern Towhee (*Pipilo erythrophthalmus*) at Stephens. Larval ticks comprised 85.0% of all ticks collected; the remainder 14.6% were nymphs (Table 10; Figs. 20, 21).

Of all ticks collected (*n=799*), 81.5% were *H. leporispalustris*, followed by 7.2% *I. brunneus*, 4.1% *I. scapularis*, 3.6% *I. dentatus*, 2.2% *I. affinis*, and 1.4% *A. americanum* (Table 10; Figs. 20, 21). Cofeeding, which occurs when more than one species of tick is found feeding on an individual bird at the same time, occurred 14.9% of the time ticks were found parasitizing captured birds, with 25 individual birds being parasitized by more than one species of tick at a given time. The most common cofeeding occurred between *I. affinis* and *I. scapularis* (20.0% of the 14.9% of cofeeding occurrences) on five different birds.

At the three sites used for these analyses, 20.4% (*n=822*) of birds captured were parasitized by at least one tick (Fig. 22). When including only species where at least 15 individuals were caught, the five most abundant species captured with ticks were: Carolina Wren (*n=118*; 52.5%), Brown Thrasher (*n=64*; 40.6%), White-throated Sparrow (*n=73*; 31.5%), Hermit Thrush (*n=18*; 16.7%), and American Robin (*n=28*; 14.3%).

For the following analyses, I used only data from the three permanent field sites (Hoffler, Jacobson, and Stephens) where ticks were commonly found and excluded any season where less than 15 ticks were collected for all analyses except the seasonality analysis. While eliminating sites and seasons may potentially cause an overestimation of tick parasitism rates, this trade-off seemed appropriate to avoid underestimating tick parasitism rates in areas where ticks occur. Because either zero or only a few ticks were found at Weyanoke and Paradise, keeping them in these analyses would weaken any relationship between tick presence and various

Table 10. Number of ticks by species and life stage collected from birds at Hoffler, Jacobson, and Stephens.

Tick Species	Common Name	# Larvae (%)	# Nymph (%)	# Adult (%)	Total # (%)
Amblyomma americanum	Lone star tick	2 (0.3)	9 (7.7)	0 (0.0)	11 (1.4)
Ixodes scapularis	Blacklegged tick	18 (2.6)	15 (12.8)	0 (0.0)	33 (4.1)
Ixodes affinis	N/A	15 (2.2)	3 (2.6)	0 (0.0)	18 (2.2)
Ixodes dentatus	N/A	29 (4.3)	0 (0.0)	0 (0.0)	29 (3.6)
Ixodes brunneus	Bird tick	46 (6.8)	12 (10.3)	0 (0.0)	58 (7.2)
Haemaphysalis leporispalustris	Rabbit tick	569(83.8)	78 (66.7)	3 (0.4)	650 (81.5)
Total	N/A	679(85.0)	117(14.6)	3 (0.4)	799(100.0)

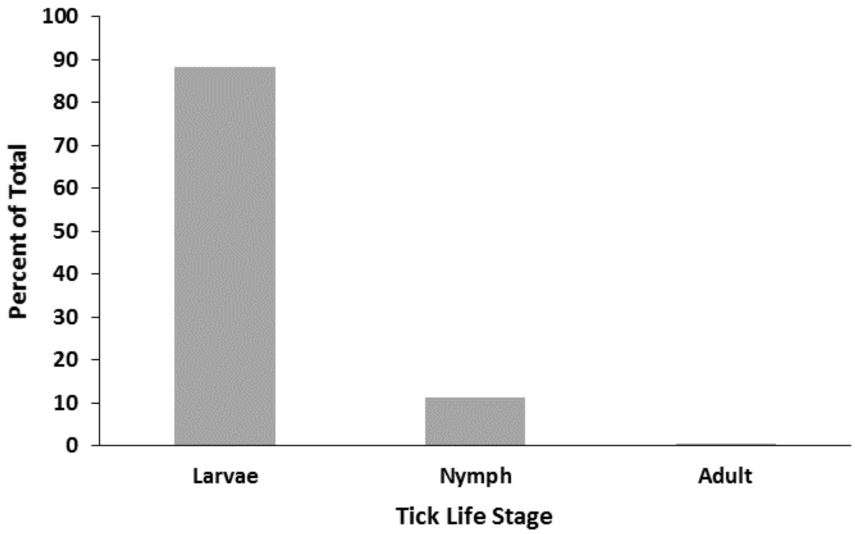

Figure 20. Percent by tick life stage parasitizing birds at Hoffler, Jacobson, and Stephens. N = 799.

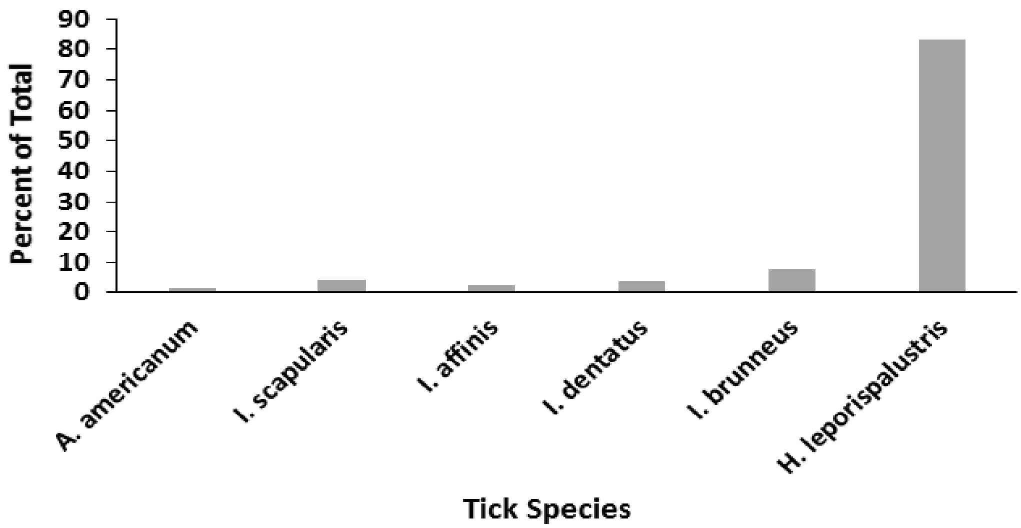

Figure 21. Percent of ticks parasitizing birds by tick species at Hoffler, Jacobson, and Stephens. N = 799.

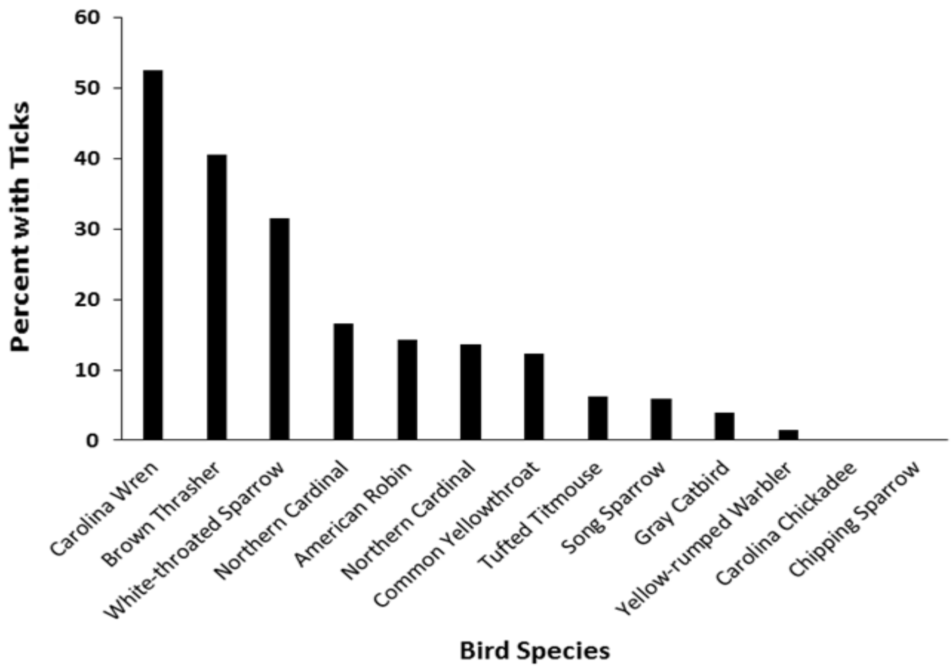

Figure 22. Percent of birds caught that were parasitized by at least one tick from August 2012-August 2014 at Hoffler, Jacobson, and Stephens in decreasing order of total birds caught. Minimum of n=15 birds is presented. N = 647.

phenological patterns. Migration analyses were limited to only the months falling in the fall and spring migrations.

All years were combined (year was defined as a calendar year) because there was no significant year effect (Wald=4.575, df=2, P=0.102). Hoffler, Jacobson, and Stephens were also combined as site effect among the three was not significant (Wald=5.648, df=2, P=0.059).

GROUND FORAGING HYPOTHESIS

Using only the three sites where ticks were consistently collected and eliminating the winter season, 642 birds were used for this analysis (Table 11). Of the ground foraging birds caught, 29.8% (*n=447*) were parasitized by ticks, 5.9% (*n=187*) of the foliage foraging birds were parasitized by ticks, and 0.0% (*n=8*) of the aerial foragers were parasitized by ticks (Fig. 23). Because zero aerial foragers were parasitized, I eliminated these birds from this analysis. There was a highly significant overall effect of foraging guild on tick parasitism with ground foraging birds being more likely to be parasitized by ticks than foliage foraging birds. (Wald=34.127, df=1, Exp(B)=6.756, P<0.001).

GROUND NESTING HYPOTHESIS

Using only the three sites where ticks were consistently collected and eliminating any birds not caught during the March to June breeding season when birds were nesting (Table 11), of the 228 birds caught, 21.2% (*n=33*) of ground

Table 11. The nesting and foraging guilds for each avian species caught. Information collected from and Ehrlich et al. 1988 and Cornell Lab of Ornithology (2015). Cavity nesters were classified as canopy nesters for this study.

Family	Scientific Name	Common Name	Nesting Guild	Foraging Guild
Columbidae	*Zenaida macroura*	Mourning Dove	Canopy	Ground
Cuculidae	*Coccyzus americanus*	Yellow-billed Cuckoo	Canopy	Foliage
Trochilidae	*Archilochus colubris*	Ruby-throated Hummingbird	Canopy	Aerial
Accipitridae	*Accipiter striatus*	Sharp-shinned Hawk	Canopy	Aerial
Picidae	*Dryocopus pileatus*	Pileated Woodpecker	Canopy	Foliage
Picidae	*Melanerpes carolinus*	Red-bellied Woodpecker	Canopy	Foliage
Picidae	*Colaptes auratus*	Northern Flicker	Canopy	Ground
Tyrannidae	*Empidonax oberholseri*	Dusky Flycatcher	Shrub	Aerial
Tyrannidae	*Sayornis phoebe*	Eastern Phoebe	Canopy	Aerial
Tyrannidae	*Myiarchus crinitus*	Great Crested Flycatcher	Canopy	Aerial
Tyrannidae	*Empidonax traillii sp.*	“Traill’s” Flycatcher	Shrub	Aerial
Vireonidae	*Vireo solitarius*	Blue-headed Vireo	Canopy	Foliage
Vireonidae	*Vireo olivaceus*	Red-eyed Vireo	Canopy	Foliage
Vireonidae	*Vireo griseus*	White-eyed Vireo	Shrub	Foliage
Corvidae	*Cyanocitta cristata*	Blue Jay	Canopy	Ground
Paridae	*Poecile carolinensis*	Carolina Chickadee	Canopy	Foliage
Paridae	*Baeolophus bicolor*	Tufted Titmouse	Canopy	Foliage
Sittidae	*Sitta canadensis*	Red-breasted Nuthatch	Canopy	Foliage
Certhiidae	*Certhia americana*	Brown Creeper	Canopy	Foliage
Troglodytidae	*Thryothorus ludovicianus*	Carolina Wren	Canopy	Ground
Troglodytidae	*Troglodytes aedon*	House Wren	Canopy	Foliage
Troglodytidae	*Troglodytes hiemalis*	Winter Wren	Canopy	Ground

Table 11
Continued

Regulidae	*Regulus satrapa*	Golden-crowned Kinglet	Canopy	Foliage
Regulidae	*Regulus calendula*	Ruby-crowned Kinglet	Canopy	Foliage
Turdidae	*Turdus migratorius*	American Robin	Canopy	Ground
Turdidae	*Catharus minimus*	Gray-cheeked Thrush	Shrub	Ground
Turdidae	*Catharus guttatus*	Hermit Thrush	Ground	Ground
Turdidae	*Catharus ustulatus*	Swainson's Thrush	Shrub	Foliage
Turdidae	*Catharus fuscescens*	Veery	Ground	Ground
Turdidae	*Hylocichla mustelina*	Wood Thrush	Canopy	Ground
Mimidae	*Toxostoma rufum*	Brown Thrasher	Shrub	Ground
Mimidae	*Dumetella carolinensis*	Gray Catbird	Shrub	Ground
Mimidae	*Mimus polyglottos*	Northern Mockingbird	Shrub	Ground
Parulidae	*Seiurus aurocapilla*	Ovenbird	Ground	Ground
Parulidae	*Setophaga ruticilla*	American Redstart	Canopy	Foliage
Parulidae	*Setophaga castanea*	Bay-breasted Warbler	Canopy	Foliage
Parulidae	*Mniotilta varia*	Black-and-white Warbler	Ground	Foliage
Parulidae	*Setophaga striata*	Blackpoll Warbler	Canopy	Foliage
Parulidae	*Setophaga caerulescens*	Black-throated Blue Warbler	Shrub	Foliage
Parulidae	*Vermivora cyanoptera*	Blue-winged Warbler	Ground	Foliage
Parulidae	*Geothlypis trichas*	Common Yellowthroat	Shrub	Foliage
Parulidae	*Setophaga citrina*	Hooded Warbler	Shrub	Foliage
Parulidae	*Geothlypis formosa*	Kentucky Warbler	Ground	Ground
Parulidae	*Setophaga magnolia*	Magnolia Warbler	Ground	Ground

Table 11
Continued

Parulidae	*Dendroica coronata coronata*	Yellow-rumped Warbler	Canopy	Foliage
Parulidae	*Setophaga Americana*	Northern Parula	Canopy	Foliage
Parulidae	*Parkesia noveboracensis*	Northern Waterthrush	Ground	Ground
Parulidae	*Vermivora celata*	Orange-crowned Warbler	Ground	Foliage
Parulidae	*Setophaga pinus*	Pine Warbler	Canopy	Foliage
Parulidae	*Setophaga discolor*	Prairie Warbler	Shrub	Foliage
Parulidae	*Protonotaria citrea*	Prothonotary Warbler	Canopy	Foliage
Parulidae	*Limnothlypis swainsonii*	Swainson's Warbler	Shrub	Ground
Parulidae	*Icteria virens*	Yellow-breasted Chat	Shrub	Foliage
Emberizidae	*Spizella passerina*	Chipping Sparrow	Shrub	Ground
Emberizidae	*Junco hyemalis*	Dark-eyed Junco	Ground	Ground
Emberizidae	*Pipilo erythrophthalmus*	Eastern Towhee	Ground	Ground
Emberizidae	*Spizella pusilla*	Field Sparrow	Ground	Ground
Emberizidae	*Passerella iliaca*	Fox Sparrow	Ground	Ground
Emberizidae	*Melospiza melodia*	Song Sparrow	Shrub	Ground
Emberizidae	*Melospiza georgiana*	Swamp Sparrow	Shrub	Ground
Emberizidae	*Zonotrichia albicollis*	White-throated Sparrow	Ground	Ground
Cardinalidae	*Passerina caerulea*	Blue Grosbeak	Shrub	Ground
Cardinalidae	*Passerina cyanea*	Indigo Bunting	Shrub	Foliage
Cardinalidae	*Cardinalis cardinalis*	Northern Cardinal	Shrub	Ground
Cardinalidae	*Pirange Rubra*	Summer Tanager	Canopy	Foliage
Icteridae	*Molothrus ater*	Brown-headed Cowbird	Canopy	Ground
Icteridae	*Quiscalus quiscula*	Common Grackle	Canopy	Ground
Icteridae	*Agelaius phoeniceus*	Red-winged Blackbird	Shrub	Ground
Fringillidae	*Carduelis tristis*	American Goldfinch	Shrub	Foliage

Table 11
Continued

Fringillidae	*Carpodacus mexicanus*	House Finch	Canopy	Ground
Sturnidae	*Sturnus vulgaris*	European Starling	Canopy	Ground

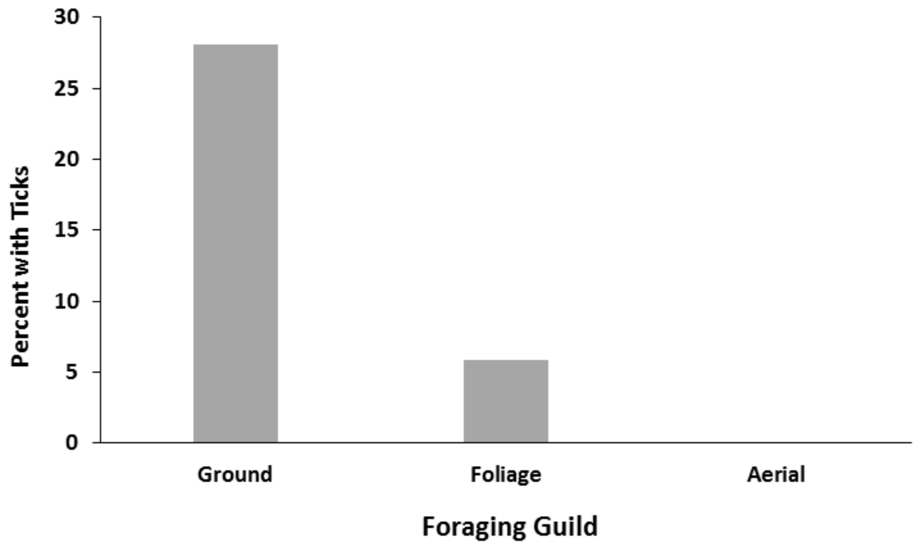

Figure 23. Percent of birds parasitized by ticks by foraging guild at Hoffler, Jacobson, and Stephens. N = 642.

nesting birds were parasitized by ticks, 14.8% (*n=115*) of shrub-nesting birds were parasitized by ticks, and 8.8% (*n=80*) of canopy nesters were parasitized by ticks (Fig. 24). There was no significant effect of nesting guild on the likelihood of a bird being parasitized (Wald=1.851, df=2, P=0.604), therefore, further analyses were not pursued.

MIGRATORY BIRD HYPOTHESIS

Using only data collected during fall (August to October) and spring migrations (March to May), 27.0% (*n=319*) of resident birds were parasitized, whereas 17% (*n=212*) of migratory birds were parasitized (Table 12; Fig. 25). During the fall migration, 28.7% (*n=349*) of birds caught were parasitized by ticks, whereas 12.1% (*n=182*) birds caught during the spring migration had ticks (Fig. 26). When combining migration status and time, 35.3% (*n=207*) of fall residents, 11.6% (*n=112*) of spring residents, 19.0% (*n=142*) of fall migrants, and 12.9% (*n=70*) of spring migrants were parasitized by at least one tick (Fig. 27).

Overall, more migrants (*n=104,* 50.0%; *n=137*, 51.3%) were sampled at the most rural sites, Jacobson and Stephens respectively, than at other sites. Hoffler, the suburban site, yielded 116 migrants caught (33.1%), whereas Paradise yielded 167 migrants (47.6%). Weyanoke, the most urban site, only yielded 59 migrants (19.9%). Generally, these data show that migrants are more commonly caught at more rural sites. Additionally, more juvenile migrants were found at rural sites than at urban sites (Weyanoke=17.2%, Paradise=17.6%, Hoffler=33.6%,

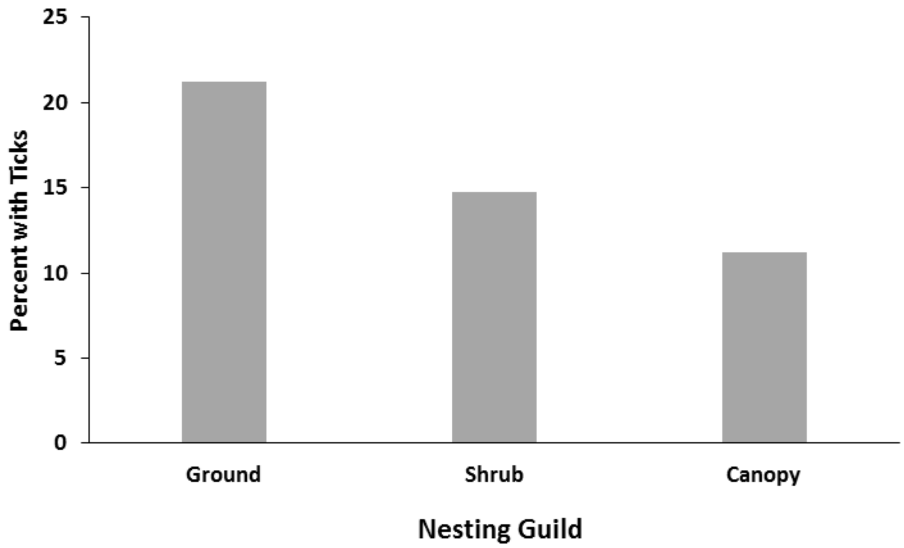

Figure 24. Percent of birds parasitized by ticks by nesting guild during the breeding season at Hoffler, Jacobson, and Stephens. N = 228.

Table 12. The migratory status and period for each avian species caught. Information collected from the Cornell Lab of Ornithology (2015).

Order	Common Name	Migration Status	Migration Time
Columbidae	Mourning Dove	Resident	N/A
Cuculidae	Yellow-billed Cuckoo	Migratory	Fall
Trochilidae	Ruby-throated Hummingbird	Migratory	Spring
Accipitridae	Sharp-shinned Hawk	Resident	N/A
Picidae	Pileated Woodpecker	Resident	N/A
Picidae	Red-bellied Woodpecker	Resident	N/A
Picidae	Northern Flicker	Resident	N/A
Tyrannidae	Dusky Flycatcher	Migratory	Spring
Tyrannidae	Eastern Phoebe	Resident	N/A
Tyrannidae	Great Crested Flycatcher	Migratory	Spring
Tyrannidae	“Traill’s” Flycatcher	Migratory	Spring
Vireonidae	Blue-headed Vireo	Migratory	Spring
Vireonidae	Red-eyed Vireo	Migratory	Spring
Vireonidae	White-eyed Vireo	Migratory	Spring
Corvidae	Blue Jay	Resident	N/A
Paridae	Carolina Chickadee	Resident	N/A
Paridae	Tufted Titmouse	Resident	N/A
Sittidae	Red-breasted Nuthatch	Migratory	Fall
Certhiidae	Brown Creeper	Migratory	Fall
Troglodytidae	Carolina Wren	Resident	N/A
Troglodytidae	House Wren	Migratory	Spring
Troglodytidae	Winter Wren	Migratory	Fall
Regulidae	Golden-crowned Kinglet	Migratory	Fall
Regulidae	Ruby-crowned Kinglet	Migratory	Fall
Turdidae	American Robin	Resident	N/A
Turdidae	Gray-cheeked Thrush	Migratory	Fall
Turdidae	Hermit Thrush	Migratory	Fall
Turdidae	Swainson’s Thrush	Migratory	Fall
Turdidae	Veery	Migratory	Fall
Turdidae	Wood Thrush	Migratory	Spring
Mimidae	Brown Thrasher	Resident	N/A
Mimidae	Gray Catbird	Resident	N/A
Mimidae	Northern Mockingbird	Resident	N/A
Parulidae	Ovenbird	Migratory	Fall
Parulidae	American Redstart	Migratory	Fall
Parulidae	Bay-breasted Warbler	Migratory	Fall

Table 12
Continued

Parulidae	Black-and-white Warbler	Migratory	Fall
Parulidae	Black-throated Blue Warbler	Migratory	Fall
Parulidae	Blue-winged Warbler	Migratory	Fall
Parulidae	Common Yellowthroat	Migratory	Fall
Parulidae	Hooded Warbler	Migratory	Fall
Parulidae	Kentucky Warbler	Migratory	Fall
Parulidae	Magnolia Warbler	Migratory	Fall
Parulidae	Yellow-rumped Warbler	Migratory	Fall
Parulidae	Northern Parula	Migratory	Fall
Parulidae	Northern Waterthrush	Migratory	Fall
Parulidae	Orange-crowned Warbler	Migratory	Fall
Parulidae	Pine Warbler	Migratory	Fall
Parulidae	Prairie Warbler	Migratory	Fall
Parulidae	Prothonotary Warbler	Migratory	Fall
Parulidae	Swainson's Warbler	Migratory	Fall
Parulidae	Yellow-breasted Chat	Migratory	Fall
Emberizidae	Chipping Sparrow	Migratory	Spring
Emberizidae	Dark-eyed Junco	Migratory	Fall
Emberizidae	Eastern Towhee	Resident	N/A
Emberizidae	Field Sparrow	Resident	N/A
Emberizidae	Fox Sparrow	Migratory	Fall
Emberizidae	Song Sparrow	Resident	N/A
Emberizidae	Swamp Sparrow	Migratory	Fall
Emberizidae	White-throated Sparrow	Migratory	Fall
Cardinalidae	Blue Grosbeak	Migratory	Spring
Cardinalidae	Indigo Bunting	Migratory	Spring
Cardinalidae	Northern Cardinal	Resident	N/A
Cardinalidae	Summer Tanager	Migratory	Spring
Icteridae	Brown-headed Cowbird	Resident	N/A
Icteridae	Common Grackle	Resident	N/A
Icteridae	Red-winged Blackbird	Resident	N/A
Fringillidae	American Goldfinch	Resident	N/A
Fringillidae	House Finch	Resident	N/A
Sturnidae	European Starling	Resident	N/A

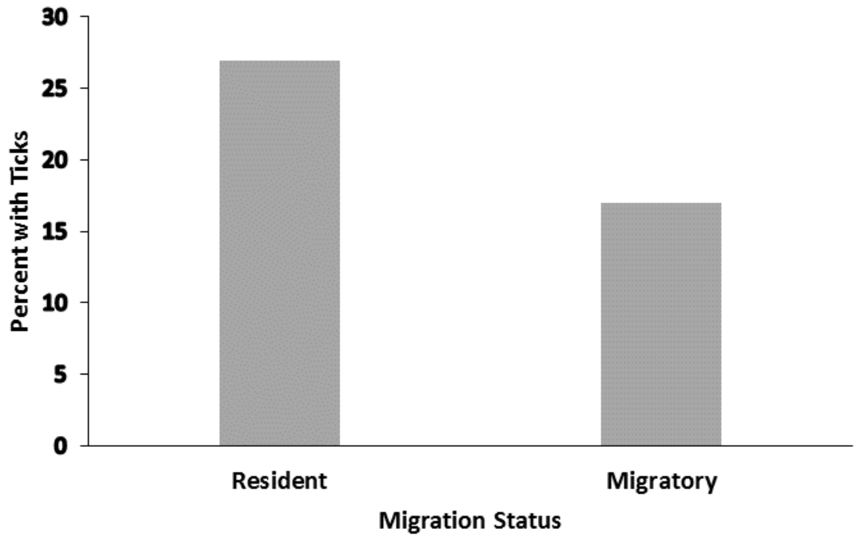

Figure 25. Percent of birds parsitized by ticks by migratory status at Hoffler, Jacobson, and Stephens. N = 531.

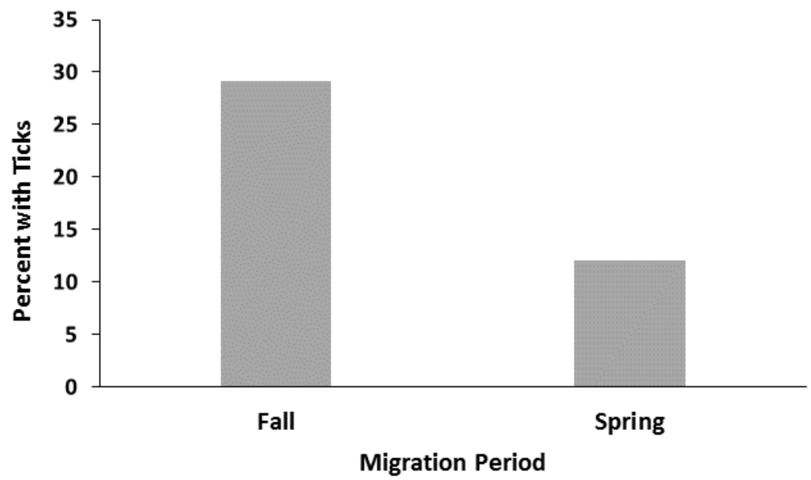

Figure 26. Percent of birds parasitized by ticks by migration time at Hoffler, Jacobson, and Stephens. N = 531.

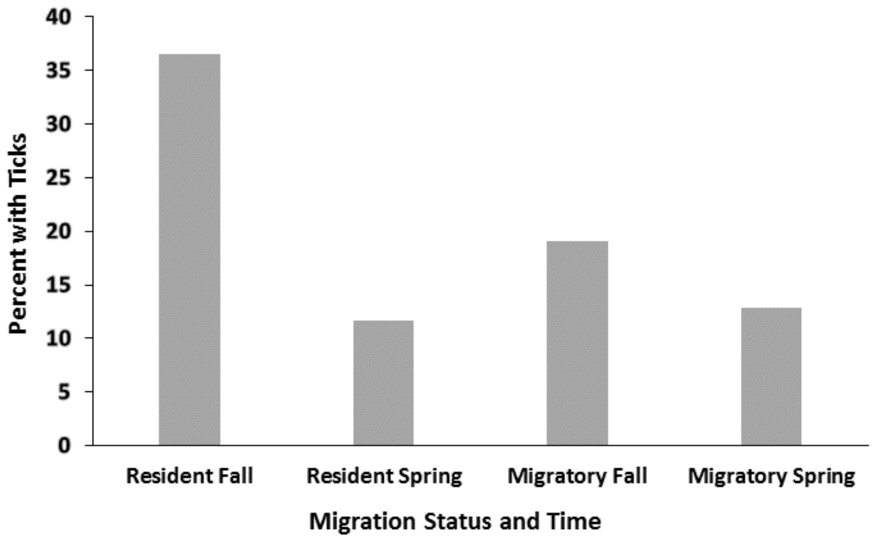

Figure 27. Percent of birds parasitized by ticks by migration status and time time at Hoffler, Jacobson, and Stephens. N = 531.

Jacobson=51.3%, Stephens=41.4%). Resident birds were more commonly parasitized by ticks than migratory birds during both migration periods (Wald=7.056, df=1, Exp(B)=1.805, P=0.008). More birds (both resident and migratory) were parasitized during fall migrations than those during the spring (Wald=17.481, df=1, Exp(B)=2.921, P<0.001). The most likely group to be parasitized was fall residents, such as the Carolina Wren and Brown Thrasher (Tables 13, 14; Fig. 27). Fourteen migratory birds served as hosts to ticks of the *Ixodes* genus, including 1 Common Yellowthroat, 5 White-throated Sparrows, 3 Hermit Thrushes, 2 Swamp Sparrows, 1 Winter Wren, and 2 Ovenbirds. Only one of these migrants was parasitized by two tick species.

In order to tease apart these data further, I addressed the above questions looking only at ground foraging birds during fall and spring migrations. One-hundred and six individuals within the ground foraging guild were caught during fall and spring migrations, 43.4% of these were parasitized by ticks. Resident birds comprised 93.4% (*n=106*) of these individuals, where only 6.6% were migrants. During fall migration, 72 (67.9%) individuals in the ground foraging guild were caught, of which, 54.1% of those caught in the fall were parasitized by at least 1 tick, all of which were residents. During spring migration, 34 individuals were caught, 20.6% of which were parasitized. All of the parasitized birds caught during spring migration were residents. Due to the low sample size of ground foraging migrants, I did not pursue this analysis.

Table 13. Number of birds caught at each field site with tick burden. WS = Weyanoke, PC = Paradise, HC = Hoffler, JC = Jacobson, ST = Stephens.

Order	Common Name	WS	PC	HC	JC	ST	# Birds with Ticks	Total Ticks Collected
Columbidae	Mourning Dove			3				
Cuculidae	Yellow-billed Cuckoo			1				
Trochilidae	Ruby-throated Hummingbird	1	1		1	1		
Accipitridae	Sharp-shinned Hawk				2		1	
Picidae	Pileated Woodpecker					1		
Picidae	Red-bellied Woodpecker				1			
Picidae	Northern Flicker	1		4	1	1		
Tyrannidae	Dusky Flycatcher							
Tyrannidae	Eastern Phoebe	1						
Tyrannidae	Great Crested Flycatcher	4		3				
Tyrannidae	“Traill’s” Flycatcher	1						
Vireonidae	Blue-headed Vireo	1						
Vireonidae	Red-eyed Vireo							
Vireonidae	White-eyed Vireo				2	1		
Corvidae	Blue Jay	3	3	4	2	2	2	4
Paridae	Carolina Chickadee	15	11	20	12	4		
Paridae	Tufted Titmouse	1	1	11	5	1	1	1
Sittidae	Red-breasted Nuthatch	1						
Certhiidae	Brown Creeper	2		8				
Troglodytidae	Carolina Wren	20	22	51	22	45		399
Troglodytidae	House Wren	1	2	2			1	1
Troglodytidae	Winter Wren			8			2	3
Regulidae	Golden-crowned Kinglet	3		6	1	4		
Regulidae	Ruby-crowned Kinglet	1		1		2		
Turdidae	American Robin	18	27	18	8	2	7	12
Turdidae	Gray-cheeked Thrush					1		

Table 13
Continued

Turdidae	Hermit Thrush	14	2	15	2	1	3	5
Turdidae	Swainson's Thrush	1	2	1				
Turdidae	Veery		1					
Turdidae	Wood Thrush					5		
Mimidae	Brown Thrasher	4	2	22	19	23	26	129
Mimidae	Gray Catbird	17	15	27	8	15	2	5
Mimidae	Northern Mockingbird		11			3		
Parulidae	American Redstart	1		2	3	4		
Parulidae	Bay-breasted Warbler	1						
Parulidae	Black-and-white Warbler			1	1	1		
Parulidae	Blackpoll Warbler					1		
Parulidae	Black-throated Blue Warbler			3				
Parulidae	Blue-winged Warbler			1				
Parulidae	Common Yellowthroat	1	12	5	20	24	4	9
Parulidae	Hooded Warbler	1						
Parulidae	Kentucky Warbler							
Parulidae	Magnolia Warbler			1				
Parulidae	Yellow-rumped Warbler	3	1	28	11	28	1	3
Parulidae	Northern Parula			1	1			
Parulidae	Northern Waterthrush					6	2	3
Parulidae	Orange-crowned Warbler	1		1				
Parulidae	Pine Warbler			2	1			
Parulidae	Prairie Warbler					1		
Parulidae	Prothonotary Warbler							
Parulidae	Swainson's Warbler					3	3	34
Parulidae	Yellow-breasted Chat		1	1		1		
Emberizidae	Chipping Sparrow		2		20			
Emberizidae	Dark-eyed Junco				12		1	1
Emberizidae	Eastern Towhee	3		3	3	8	6	21
Emberizidae	Field Sparrow		10	1	1			
Emberizidae	Fox Sparrow	3	2	1		1		

Table 13
Continued

Emberizidae	Song Sparrow	23	11	4	2			1
Emberizidae	Swamp Sparrow		6	3		4	3	
Emperizidae	White-throated Sparrow	18	38	14	18	41	21	54
Cardinalidae	Blue Grosbeak		3					
Cardinalidae	Indigo Bunting		22		6	1	1	1
Cardinalidae	Northern Cardinal	121	39	59	15	21	10	12
Cardinalidae	Summer Tanager			1				
Icteridae	Brown-headed Cowbird		1				62	
Icteridae	Common Grackle		4		1		1	1
Icteridae	Red-winged Blackbird		1	3				
Fringillidae	American Goldfinch		69				0	
Fringillidae	House Finch	33						
Sturnidae	European Starling		14					

Table 14. Tick burdens found on each avian species caught at Hoffler, Jacobson, and Stephens.

Order	Common Name	# Caught	% Birds Parasitized	Max # Ticks on 1 Bird
Columbidae	Mourning Dove	3	0.00	0
Cuculidae	Yellow-billed Cuckoo	1	0.00	0
Trochilidae	Ruby-throated Hummingbird	3	0.00	0
Accipitridae	Sharp-shinned Hawk	2	0.00	0
Picidae	Downy Woodpecker	4	0.00	0
Picidae	Pileated Woodpecker	1	0.00	0
Picidae	Red-bellied Woodpecker	1	0.00	0
Picidae	Yellow-shafted Northern Flicker	8	0.00	0
Vireonidae	White-eyed Vireo	3	0.00	0
Corvidae	Blue Jay	8	25.0	3
Paridae	Carolina Chickadee	36	0.00	0
Paridae	Tufted Titmouse	16	0.06	1
Certhiidae	Brown Creeper	8	0.00	0
Troglodytidae	Winter Wren	9	22.2	2
Troglodytidae	Carolina Wren	118	52.5	57
Troglodytidae	House Wren	2	50.0	1
Regulidae	Golden-crowned Kinglet	11	0.00	0
Regulidae	Ruby-crowned Kinglet	4	0.00	0
Turdidae	American Robin	28	14.3	3
Turdidae	Gray-cheeked Thrush	1	0.00	1
Turdidae	Hermit Thrush	18	16.7	3
Turdidae	Swainson's Thrush	1	0.00	0
Turdidae	Wood Thrush	5	20.0	0
Mimidae	Brown Thrasher	64	40.6	100
Mimidae	Gray Catbird	50	4.00	4
Mimidae	Northern Mockingbird	4	0.00	0
Parulidae	Ovenbird	7	28.6	3
Parulidae	American Redstart	9	0.00	1
Parulidae	Black-and-white Warbler	3	0.00	0
Parulidae	Blackpoll Warbler	1	0.00	0
Parulidae	Black-throated Blue Warbler	3	0.00	0
Parulidae	Blue-winged Warbler	1	0.00	0
Parulidae	Hooded Warbler	1	0.00	0

Table 14
Continued

Parulidae	Yellow-rumped Warbler	67	1.49	3
Parulidae	Northern Parula	2	0.00	0
Parulidae	Northern Waterthrush	6	33.3	2
Parulidae	Orange-crowned Warbler	1	0.00	0
Parulidae	Pine Warbler	3	0.00	0
Parulidae	Prairie Warbler	1	0.00	0
Parulidae	Swainson’s Warbler	3	0.00	18
Parulidae	Yellow-breasted Chat	2	0.00	0
Emberizidae	Chipping Sparrow	20	0.00	0
Emberizidae	Dark-eyed Junco	12	16.6	6
Emberizidae	Eastern Towhee	14	42.9	14
Emberizidae	Field Sparrow	2	0.00	0
Emberizidae	Fox Sparrow	3	0.00	0
Emberizidae	Song Sparrow	17	5.88	13
Emberizidae	Swamp Sparrow	7	42.9	3
Emberizidae	White-throated Sparrow	73	31.5	10
Cardinalidae	Indigo Bunting	7	14.3	1
Cardinalidae	Northern Cardinal	95	13.7	8
Cardinalidae	Summer Tanager	1	0.00	0
Icteridae	Common Grackle	1	0.00	1
Icteridae	Red-winged Blackbird	3	0.00	0
Sturnidae	European Starling	2	0.00	0

DIRTY JUVENILE HYPOTHESIS

Of all 822 captures, 37.3% were juvenile, 53.8% were adult, and 8.9% were of unknown age. Of all birds caught, 26.3% (*n=81*) of juvenile birds, 18.2% (*n=81*) of adult birds, and 8.2% (*n=6*) of unknown age were parasitized by at least 1 tick (Fig. 28). For statistical analyses, I eliminated birds of unknown age. Juvenile birds were more commonly parasitized than adult birds (Wald=6.919, df=1, Exp(B)=1.600, P=0.009).

DIRTY MALE HYPOTHESIS

Throughout the duration of the study for the 3 sites used for these analyses, of the 822 birds caught, 24.1% were male, 17.2% were female, and 58.7% were of unknown sex. Of all birds parasitized by at least 1 tick (*n=157*), 14.6% were male, 11.3% were female, and 25.4% were of unknown sex (Fig. 29). For statistical analyses, birds of unknown sex were eliminated. There was no significant difference in the effect of bird sex on tick parasitism rates between males and females year-round (Wald=0.786, df=1, Exp(B)=1.344, P=0.744).

In order to examine the relationship between bird sex and tick parasitism rates during the breeding season, data were partitioned further by eliminating any birds that were not caught during the March to June breeding season. Two-hundred and thirty birds were sampled, of which 33.5% were male, 23.0% were female, and 43.5% were of unknown sex. Thirty-three (14.3%) of all birds caught within these constraints were parasitized. During the breeding season, 14.3% of males were

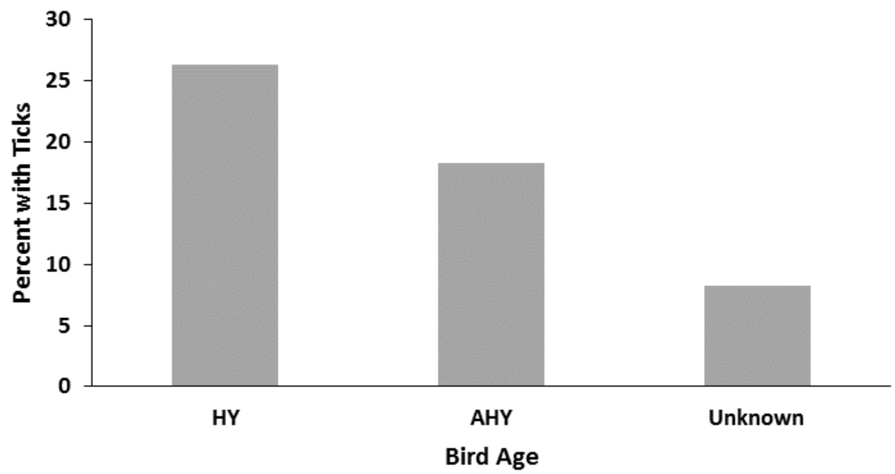

Figure 28. Percent of birds parasitized by ticks by age at Hoffler, Jacobson, and Stephens. HY = hatch-year, AHY = after-hatch-year. N = 822.

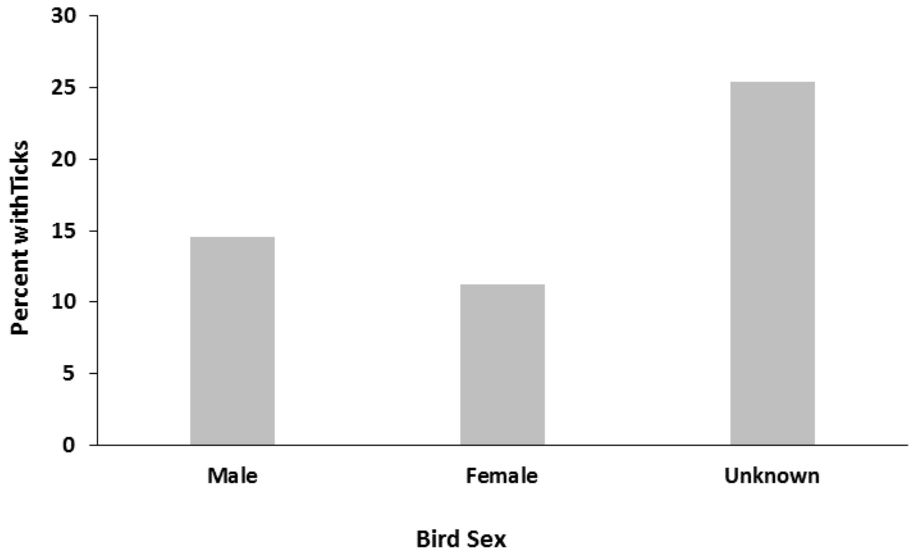

Figure 29. Percent of birds parasitized by ticks by sex at Hoffler, Jacobson, and Stephens. N = 822.

parasitized by ticks, 13.2% of females were parasitized, and 15.0% of birds of unknown sex were parasitized. For this analyses, birds of unknown sex were eliminated. There was also no significant difference in the effect of bird sex on tick parasitism rates between males and females during the breeding season (Wald=0.031, df=1, Exp(B)=0.913, P=0.861).

BIRD WEIGHT HYPOTHESIS

Bird weight had no significant effect on the likelihood of a bird being parasitized when using linear (Wald=1.297, P=0.195; Figure 30), quadratic (Wald=-1.516, P=0.130; Figure 31), or polynomial predictions (Wald=0.698, P=0.485; Figure 32).

TICK STAGE HYPOTHESIS

The majority (85%; *n=679*) of all ticks collected were in their larval stage, followed by 14.6% (*n=117*) of nymphs. Only 0.4% (*n=3*) were adult (Table 10; Fig. 20). Of the ticks most commonly collected the genus *Ixodes*, nine larval *I. brunneus* parasitized six individual birds, and ten *I. brunneus* nymphs parasitized two individual birds (Table 15).

TICK SEASONALITY HYPOTHESIS

Birds parasitized by ticks were most commonly caught during the fall (September to November), followed by the summer (June to August; Fig. 33). In the winter, 13.2% (*n=181*) of birds caught were parasitized by at least one tick, 12.1% (*n=182*) in the spring, 23.1% (*n=194*) in the summer, and 28.9% (*n=263*) in the fall. The effect of season on a bird being parasitized by a tick was highly significant (Wald=24.982, df=3, P<0.001).

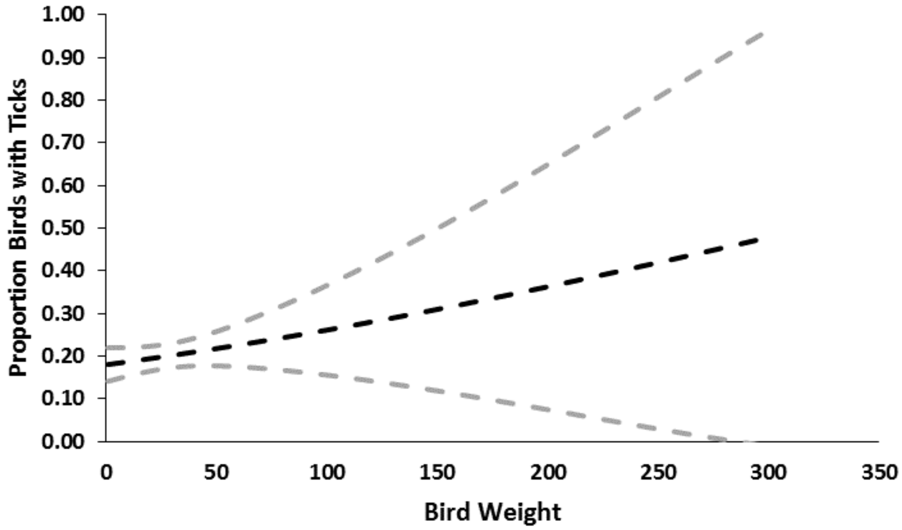

Figure 30: Linear model prediction estimates of the proportion of birds parasitized by ticks based on bird weight. Dotted lines indicate unconditional standard errors around predictions.

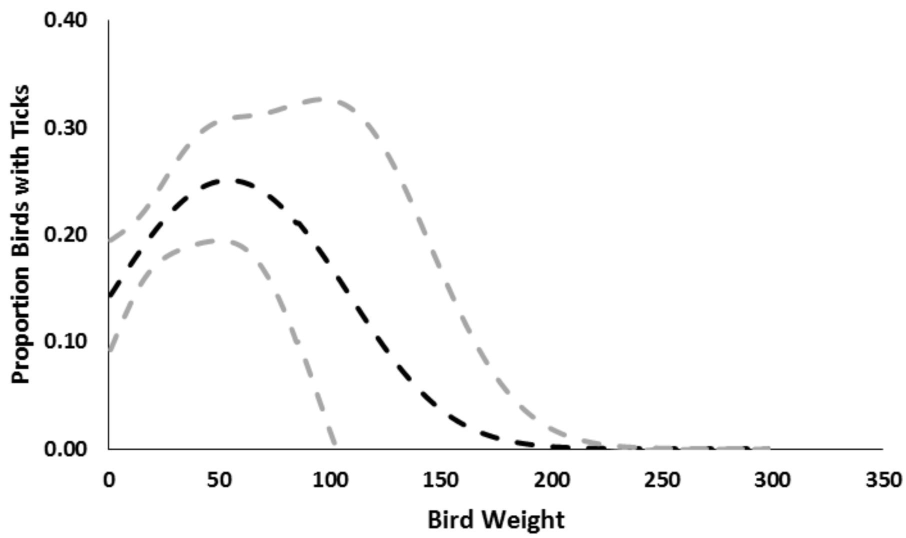

Figure 31: Quadratic model prediction estimates of the proportion of birds parasitized by ticks based on bird weight. Dotted lines indicate unconditional standard errors around predictions.

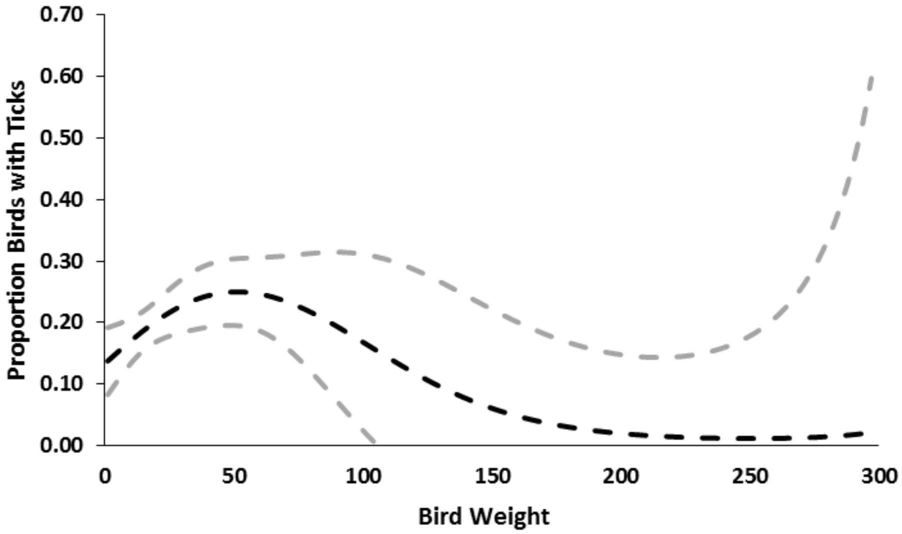

Figure 32: Polynomial model prediction estimates of the proportion of birds parasitized by ticks based on bird weight. Dotted lines indicate unconditional standard errors around predictions.

Table 15: Migratory birds parasitized with Ixodid ticks. ID = *I. dentatus*, IA = *I. affinis*, IB = *I. brunneus*, IS = *I. scapularis*. COYE = Common Yellowthroat, WTSP = White-throated Sparrow, HETH = Hermit Thrush, SWSP = Swamp Sparrow, WIWR = Winter Wren, OVEN = Ovenbird. ST = Stephens, HC = Hoffler, JC = Jacobson.

Host	Site	Month	ID larvae	IA larvae	IA nymphs	IB larvae	IB nymphs	IS larvae	IS nymphs	Total
COYE	ST	9		1						2
WTSP	ST	12			1					1
WTSP	HC	11				2				2
HETH	HC	11				2				2
HETH	ST	11				1				1
HETH	HC	11				1				1
WTSP	ST	12				1				1
WTSP	JC	12					1			1
WTSP	JC	12					9			9
SWSP	ST	12				2				2
WIWR	HC	11	2							2
OVEN	HC	8						2		2
SWSP	ST	4							1	1
OVEN	HC	9						2		2

Birds were more commonly parasitized in the fall than in the winter (Wald=14.369, df=1, Exp(B)=2.660, $P<0.001$), in the fall vs the spring (Wald=16.729, df=1, Exp(B)= 2.959, $P<0.001$), in the winter vs summer (Wald=5.995, df=1, Exp(B)=0.508, P=0.014), and in the spring vs summer (Wald=7.653, df=1, Exp(B)=0.456, P=0.006; Fig. 33). There was no significant difference in tick parasitism rates on birds from fall to summer (Wald=1.942, df=1, Exp(B)=1.350, P=0.163) or from winter to spring (Wald=0.113, df=1, Exp(B)= 8.197, P=0.737).

Rabbit ticks were present year-round, though in lower numbers during winter months. Rabbit tick abundance on birds peaked in September for both larvae and nymphs combined (Figs. 34, 35). Nymphal rabbit ticks also peaked in September. *I. brunneus* peaked in November, whereas *I. scapularis* peaked in June, and *I. dentatus* peaked in October - November. Too few *A. americanum* and *I. affinis* were collected to determine when juveniles of these species are most commonly parasitizing birds (Fig. 36).

DISCUSSION

Understanding both tick and avian phenologies is imperative to comprehending parasite-host dynamics. Ticks were most commonly found on the birds' heads and around their ears, likely because they cannot easily preen this region (Gregoire et al. 2002; Fig. 19). The most ticks were collected off Carolina Wrens, followed by Brown Thrashers (Tables 13, 14, 15). This study found that are much more commonly parasitized by ticks in their larval stage than in either nymphal or adult stages (Fig.

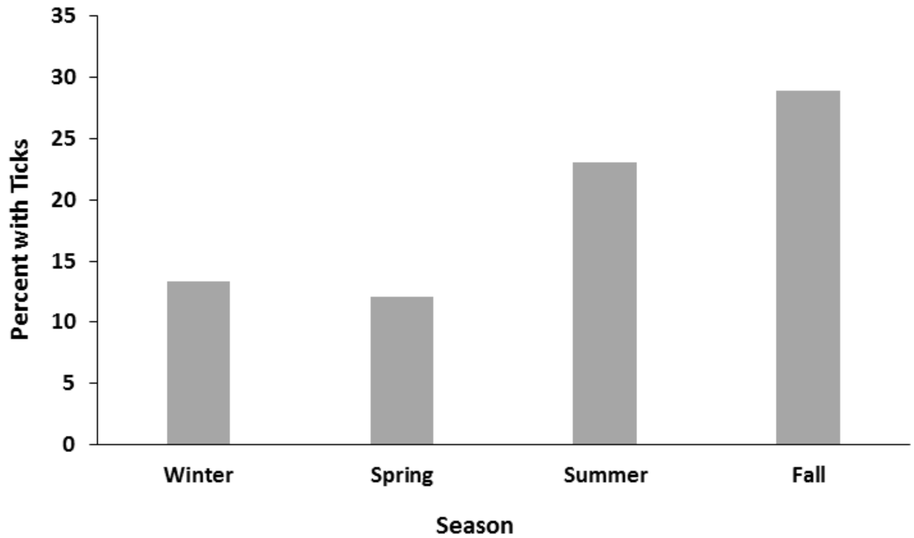

Figure 33. Percent of birds parasitized by ticks by season at Hoffler, Jacobson, and Stephens. Fall = September to November, Spring = March to May, Summer = June to August, Winter = December to February. N=822.

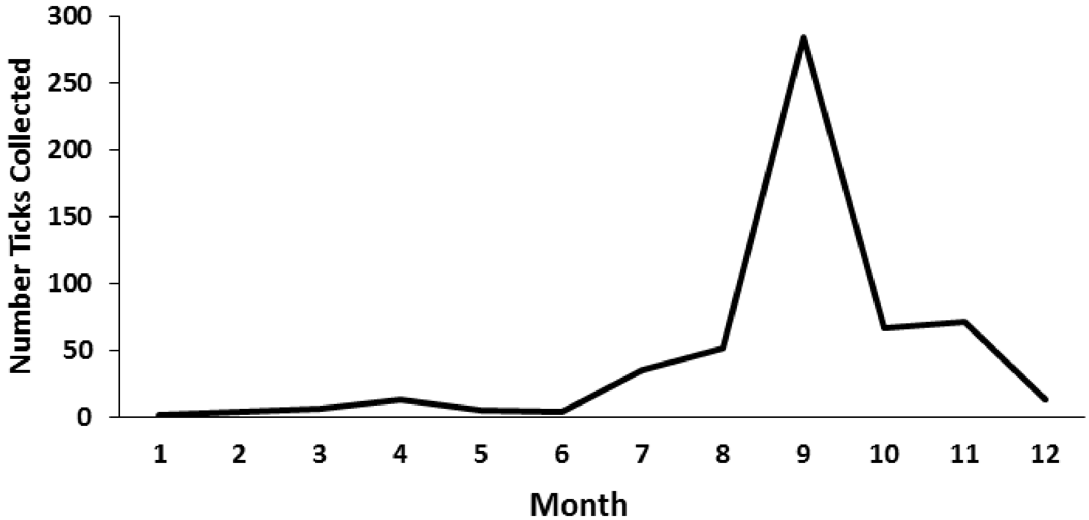

Figure 34: Rabbit tick prevalence (both larvae and nymphs) on caught birds by month (1= January to 12 = December).

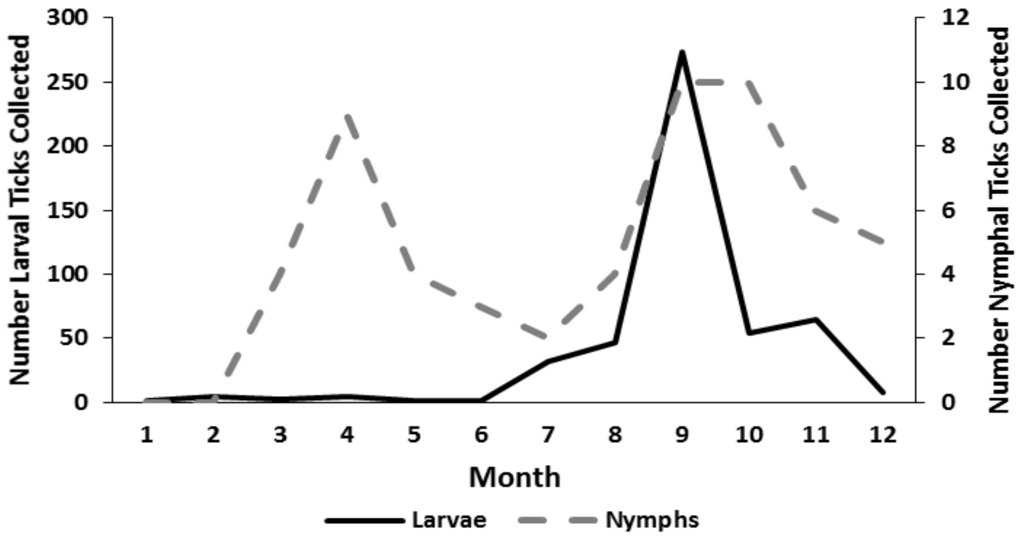

Figure 35: Rabbit tick prevalence on caught birds by month (1 = January to 12 = December).

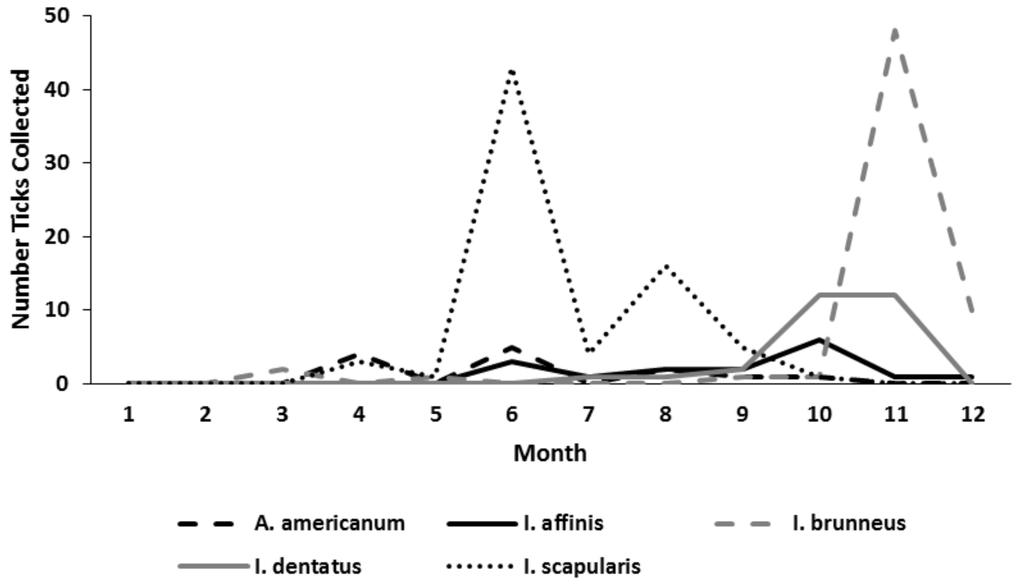

Figure 36: All ticks in all life stages other than rabbit ticks and their prevalence by month (1 = January to 12 = December)

36). Because birds, on average, are relatively small, they provide adequate sources of blood to juvenile ticks, whereas larger ticks seek larger hosts in order to meet their blood demands (Semtner and Hair 1973a,b).

GROUND FORAGING HYPOTHESIS

The ground foraging hypothesis is supported by other studies that found that ground foraging birds are more susceptible to tick parasitism than other foraging guilds (Rand et al. 1998, Peters 2009). Based on the results of this study, the ground foraging hypothesis is supported. Birds that foraged on the ground, such as Carolina Wrens, Brown Thrashers, and Northern Cardinals, were more commonly parasitized by ticks than foliage or aerial foragers (Fig. 23). Ground foragers spend a large portion of their time on or near the ground searching for food; therefore, they share the ground environment with ticks (Stafford et al. 1995, Eisen et al. 2004). The ground foraging Carolina Wren was the most commonly parasitized species caught during this study, likely because it is ubiquitous and a habitat generalist (Dickenson and Noble 1978). Because Carolina Wrens commonly share habitat with ticks, they are highly susceptible to being parasitized ticks (Rand et al. 1998).

Foliage foragers, such as the Yellow-rumped Warbler, were parasitized by ticks more commonly than aerial foragers but less commonly than ground-foragers, likely because they do not forage solely in tick habitat. This coincides with what was predicted in the ground foraging hypothesis, though it would be interesting in the future, if higher numbers of birds in different foraging guilds were caught, to separate species into more specific guilds (bark gleaners, low canopy foragers, high canopy foragers etc). This study was limited in that I simplified foraging guild analyses by only using three broad foraging categories due to the limited number of species caught in very specific guilds, such as bark gleaners.

This study also found that none of the aerial foragers caught were parasitized by ticks. Examples of aerial foragers caught during this study include the Eastern Phoebe and Great-created Flycatcher (Table 11). Neither of these species was found being parasitized by a tick during this study. Because ticks neither fly nor climb much higher than a few meters from the ground, aerial foragers are not likely to come in contact with ticks very often since they “hunt” in the air (Norberg 1986, Randolph 1998).

GROUND NESTING HYPOTHESIS

The ground nesting hypothesis suggests that birds that nest on or near the ground are more likely to be parasitized by ticks than birds that belong to other nesting guilds. This hypothesis is supported by other studies that found that since ticks live on the ground, birds that nest in tick habitat come in contact with ticks more frequently than birds that nest above the ground (Carroll et al. 1995, Semtner et al. 1971, Stafford et al. 1995). My study, however, did not support the ground nesting hypothesis statistically. I did, however, find that ground nesting birds were more commonly parasitized than both shrub nesting and canopy nesting birds during the breeding season, though not at statistically significant levels (Fig. 24). A commonly caught ground nester was the Hermit Thrush. Brown Thrashers and Northern Mockingbirds were commonly caught shrub nesters, and American Robins were commonly caught canopy nesters. Ironically, Carolina Wrens in particular were highly parasitized regardless of their nesting guild (listed as canopy for this study as cavity nesters were grouped with canopy nesters). This likely is because while the nest in shrubs, they forage on the ground and therefore still spend a lot of time sharing tick habitat. This suggests that foraging guild may be a better predictor for tick parasitism than nesting guild, as birds forage year-round, whereas they only nest during the breeding season.

Although ground foraging and ground nesting birds both were more commonly parasitized by ticks than birds in other foraging or nesting guilds, there was only a significant effect of foraging guild on tick parasitism. This could be an artifact that the nesting guild hypothesis was limited to species that nest in Virginia, whereas the foraging guild hypothesis addresses birds year-round. The nesting/breeding season in Virginia occurs in the spring, when ticks were not as commonly found on birds in general than in the summer and fall, potentially biasing analyses.

MIGRATORY BIRD HYPOTHESIS

The migratory bird hypothesis posits that migratory birds are more commonly parasitized by ticks than resident birds. Prior studies have supported this claim (Odum et al. 1961, Wilson et al. 1984, Moore and Yong 1991). The results of this study, however, refute this hypothesis as more resident birds were parasitized by ticks than migratory (Figs. 26, 27). One explanation could be that ticks are found within my study areas and are, therefore, parasitizing resident birds locally. Because it is not possible to know where migrants are coming from and since migrants often only stop in this region for a few days, they may be parasitized by local ticks but then carry these ticks to other areas along their migration route; however, because I found no non-native ticks on migrants, this explanation likely is not valid. Generally, migratory birds were more commonly caught at more rural sites, suggesting that migratory birds prefer less urbanized habitat and are less ubiquitous than resident birds that are able to live in urban areas year-round. Some studies suggest that juvenile migrants migrate later and travel closer to the coast than adults (McKinnon et al. 2014); however, this study did not support this claim as a higher percentage of juvenile birds were caught at rural sites, which tended to be more inland, than at urban sites, which tended to be more coastal.

Some examples of commonly caught resident birds included: Carolina Wren, Blue Jay (*Cyanocitta cristata*), and Brown Thrasher (Table 11). Each of these species vary in size, foraging, and nesting guilds. Carolina Wrens and Brown Thrashers were both parasitized by ticks in high numbers, while Blue Jays were less commonly parasitized. Blue Jays are canopy nesters and ground foragers (Table 11); because of this, it is relatively surprising that Blue Jays were not more commonly parasitized. A potential explanation for this finding is that Blue Jays are known to destroy other birds' nests and to eat the eggs of other birds (Bissonnette 1939). Although they are primarily ground foragers, they also appear to prey on other birds and their eggs. For this reason, they likely do not spend as much time on the ground as other ground foraging species, particularly during the breeding season.

Some examples of commonly caught migratory birds included: Hermit Thrush, White-throated Sparrow, and American Goldfinch (*Carduelis tristis;* Table 12). Hermit Thrushes and White-throated Sparrows were commonly parasitized, although American Goldfinches were not. American Goldfinches are foliage foragers and shrub nesters and thus would not commonly be found in areas with ticks (Table 11).

Another interesting result concerning migration is that significantly more birds were parasitized during the fall migration than during the spring migration (Figs. 25, 26, 27). This likely is due to the fact that female ticks often lay eggs in the summer, meaning larval ticks, which were previously shown to be the most likely life-stage on ticks, were most active during the fall (Fig. 26). Because spring migration follows the winter when fewer ticks are active, it follows that there were fewer ticks on birds during the spring migration than during the fall migration.

DIRTY JUVENILE HYPOTHESIS

The dirty juvenile hypothesis suggests that because younger birds often spend more time on the ground than their adult counterparts, they are more likely to be parasitized by ticks. This study supported this hypothesis and was in accordance to several other studies (Semtner et al. 1971, Woodward 1983, Soler 1994; Fig. 28). Because juvenile birds spend a lot of time in their nests as hatchlings and then a large amount of time on the ground as fledglings, they often share tick habitat and therefore may be more commonly parasitized than adults (Woodward 1983, Soler 1994). Another explanation of this relationship could be that young birds may not groom themselves as well as adults.

DIRTY MALE HYPOTHESIS

The dirty male hypothesis suggests that male birds are more commonly parasitized by ticks than female birds during the breeding season because birds more aggressively defend their territories and often spend more time foraging than females (Orians 1969, Hau et al. 2000, Matysiokova and Remes 2014). This study did not support this hypothesis as no significant difference was found between male and female birds both year-round and during the breeding season (Fig. 29). An explanation for the dirty male hypothesis not being supported could be that tick parasitism rates on female birds are the same as those on males. Although many passerine females spend more time in their nests than their mates, and therefore, if their nests are on or near the ground, are highly susceptible to tick parasitism while incubating (Jones 2008), males of many passerine species share parental care and assist in incubating and provisioning their young (Van Rhijn 1983). Additionally, since many passerine species share parental care, both parents contribute to fledgling care and may spend more time on or near the ground as their young learn to fly and care for themselves; increased time on or near the ground increases birds' chances of being parasitized by ticks (Holmes 1986, Jones 2008).

Another explanation could be that because the number of birds of unknown sex was high, as sexing birds outside the breeding season is difficult in many species, there was not enough data on the sex of many species outside of the breeding season to address this question (Pyle 2008, Douglas et al. 2013).

BIRD WEIGHT HYPOTHESIS

Larger, heavier birds theoretically are more commonly and more heavily parasitized by ticks than smaller birds. Larger birds emit more heat and carbon dioxide than smaller birds, making them more likely to be detected. Additionally, larger birds take up a larger surface area and therefore may be more likely to brush against ticks than birds with smaller surface areas. However, I found no significant effect of bird weight on tick parasitism rates (Figs. 30, 31, 32).

TICK SEASONALITY HYPOTHESIS

Ticks have four life stages, most of which are active at different times of year. Generally, larval and nymphal ticks are more active in summer and fall when humidity levels are high (Berger et al. 2014). Because ticks rely heavily on humidity to survive, (Altizer et al. 2006) and humidity varies seasonally (Paul and Erinle 1982), the combination of humidity and seasonality likely affects tick occurrence. Typically, in Virginia, summer is the most humid season. This coincides with the time period during which many female ticks lay their eggs, which likely is one reason why fall was the season with the highest proportion of birds caught with ticks. Eggs that were laid in the summer, hatch as larvae in the fall in time to parasitize birds. I found that there was a significant effect of seasonality on tick parasitism rates, in which the highest percentage of birds were parasitized in the fall followed by the summer; however, there were no significant differences in tick parasitism rates between the fall and summer, likely because the rates of parasitism were both relatively high.

Bird behavior varies according to time of year, in particular during the spring as they make their nests and breed. Migratory birds often are energetically active during the fall and spring as well, as they are travelling far distances in order to travel to breeding and wintering grounds. Arguably, winter is the least active season for all birds, though the colder weather likely provides other challenges to them, particularly in finding adequate food sources (Houston and McNamara 1993). Birds that are preparing to migrate, are in the middle of their migration, or birds that are not migrating but preparing for the breeding season have high energetic requirements; therefore, they must increase foraging times (Metcalfe and Furness 1984).

Understanding the relationship between birds and ticks is imperative because ticks are vectors of infectious diseases that can affect humans (Burgdorfer 1975). Since birds can transport new tick species to novel areas rapidly, investigating bird movement patterns in relation to tick parasitism prevalence on birds is of utmost importance to everyone, including the public (Hasle 2013). In addition to bringing attention to the relationship between ticks and birds, this study could help the public better appreciate why ticks are a threat. Most people associate ticks with deer and with stray dogs and cats; this study shows that even smaller animals, such as birds, are parasitized by ticks. Additionally, from an ecological perspective, the relationship between birds and ticks is interesting in that birds have the ability to bring ticks to new areas, causing tick ranges to expend (Anderson and Magnarelli 1984, Brunner and Ostfeld 2008, Peters 2009). Range expansion in many animals, not just ticks, is a commonly studied topic, especially in regards to global climate change (Ogden et al. 2006). The combination of birds' propensity to travel far distances quickly with climate change could drastically affect where ticks are able to start new populations (Anderson and Magnarelli 1984, Ogden et al. 2006).

Birds are known hosts of ticks, as are many other vertebrates, including humans (Estrada-Pena and Jongejan 1999, James et al. 2011); however, birds add complexity to the relationship between ticks and their hosts in that they migrate long distances in very short periods of times (Anderson and Magnarelli 1984). Other vertebrates also have long migrations (Scott et al 2001); however, these taxa typically do not travel as far and as quickly as birds do (Peters 2009). The importance of this lies in that this relationship between birds and ticks could enable new species of Ixodid ticks, with novel pathogens, to be introduced into novel areas very quickly (Table 15). Even birds that do not migrate often have large home-ranges and/or territories. Therefore, even resident birds can travel relatively long distances within one day (Brunner and Ostfeld 2008, Peters 2009). In addition to the potential for birds to disperse ticks and pathogens to novel areas, birds can disperse native ticks to previously uninhabited patches within their natural ranges (Anderson and Magnarelli 1984). This could increase the likelihood of humans interacting with ticks and in turn could increase the prevalence of humans contracting tick-borne diseases (Hasle 2013).

Many studies have explored the relationship between birds and ticks; however, this study is unique in that it explores this relationship year-round. The only reliable information for the ticks found in the study region of coastal southeastern Virginia is that *Ixodes scapularis* larvae are most abundant from July to September (H. Gaff, pers. comm.). No other information on the tick species within the study region is available. Ticks are active, to an extent, year-round; therefore, studying ticks and their hosts year-round is also necessary. This study, for example, collected 181 ticks during the winter months of December to February (at Hoffler, Jacobson, and Stephens during all years combined), months not typically associated with tick presence. Although ticks were found in lower numbers during the winter than during other seasons, enough ticks were collected to suggest that ticks seeking hosts in the winter is not due to random chance. Most studies have limited their scope to tick parasitism rates on birds during fall and spring migrations, likely for several reasons. One reason could be that there are hundreds of banding stations throughout North America that are only active during bird migrations (Desante et al. 2008).

While studying bird-tick relationships during migration periods is useful, these studies are biased as they do not address bird-tick patterns during the non-migratory periods of summer and winter. Many studies are also biased toward migration periods because capture rates are typically higher during these very active periods. The success rate of capturing birds in this study overall is lower than in many other studies, likely because we sampled at all times of year, rather than just during high bird movement times during peak migration. Understanding the prevalence of tick parasitism rates during non-migration periods helps fill in gaps in our knowledge.

Because most previous studies have looked at the relationship between birds and ticks during bird migration periods, this study provides novel data on tick parasitism rates on birds year-round. I found that ticks parasitize hosts during all seasons, including the winter when most assume ticks are inactive. This study shows the limitations of only addressing the bird-tick relationship at certain parts of the year. Eliminating data from non-migratory periods, such as summer and winter, causes a large gap in the scientific understanding of tick phenology and the relationship between ticks and their hosts. Additional studies addressing the tick-host relationship year-round is mandated in order to increase the scientific understanding of these relationships.

CHAPTER IV

CONCLUSIONS

Urbanization drastically affects wildlife by destroying and fragmenting the habitat they rely on, typically resulting in various species either dying out in a given area or being forced to leave in hopes of finding new suitable habitat (Bradley and Altizer 2006, Hunt et al. 2013, Schaefer and Gonzales 2013). Because of this, the relationships wildlife have with the ectoparasites, such as ticks, that rely on them to survive are also affected (Blair 1996, Fokidis et al. 2008, McKinney 2008). The interaction between landscape-level effects of urbanization and bird-tick dynamics is complex. This is in part due to the fact that what defines an area as urban or rural is highly variable and largely dependent upon relatively arbitrary criteria. The variability in life history traits of avian and tick taxa further complicates relationships. Phenology, seasonality, sex, and age, to name only a few, also likely affect the relationship between birds and ticks and the likelihood of birds being parasitized by ticks.

In Chapter II, I examined how urbanization affected tick parasitism rates on birds by using various land cover measures. The effect of impervious surface at the 500 m buffer was the best supported model when addressing the five permanent sites; impervious surface at the 500 m buffer predicted a decrease in tick parasitism with an increase in these two cover types. After removing the two permanent field sites where ticks were rarely found (Weyanoke and Paradise), season was the best predictor of tick parasitism, followed by the additive effects of season and avian species richness. By eliminating sites with very high impervious surfaces, I was able to examine other predictors that would not be swamped out by the landscape level effect of impervious surface. Previous studies have found that tick prevalence is related to the quantity of impervious surfaces and season (Arnold and Gibbons 1996, Morse et al. 2003, Bradley and Altizer 2006, Peters 2009).

I also tested the environmental and host constraint hypotheses, which pertain to how site urbanization levels affect tick prevalence. The environmental constraint hypothesis, which suggests that ticks are limited by the conditions present within the environment and therefore will only parasitize birds in areas where environmental conditions support tick life, was supported, based on the trend that very few birds were parasitized by ticks at urban sites as opposed to many birds being parasitized in more rural areas. The host constraint hypothesis, which suggested that ticks have avian host preferences and will only parasitize certain species of birds if preferred hosts were not present, was rejected, as uncommonly parasitized birds at rural sites were not parasitized at urban sites.

In Chapter III, I tested eight hypotheses that addressed the effects of both tick and avian phenology on the likelihood of birds being parasitized by ticks. While six tick species were collected from birds, larval rabbit ticks (*H. leporispalustris*) were by far the most tick parasites on birds in this region, likely because rabbit ticks are known to show preference for rabbits and birds, particularly during their juvenile life stages. Therefore, results for this study may primarily portray the relationship between birds and rabbit ticks, rather than the relationship between birds and all species of tick found in coastal southeastern Virginia. The relationship between rabbit ticks and birds is important for human health, as rabbit ticks can carry the pathogen that causes tularemia, a bacterial disease that can cause serious symptoms such as ulcers and high fever (Shah and Sunil 2013).

Additionally, ticks showed a preference for ground foraging and ground nesting species, though no statistical difference was found based on nesting guild, in accordance with the fact that birds that spend the majority of their time on or near the ground more often come in contact with questing ticks. Resident birds were more commonly parasitized than migratory birds, and birds caught during the fall migration were more commonly parasitized than those caught during the spring migration. Previous studies found the reverse result, suggesting that migratory birds were more often parasitized than resident birds due to an increase in ground foraging behavior required to build suitable fat stores (Klaassen et al. 2013). Effects of bird age and sex were also examined. Juvenile birds were more commonly parasitized than adult birds, and males were more commonly parasitized than females; however, there was no statistical difference in tick parasitism rates based on sex. Because aging birds as either juvenile or adult tends to be easier than sexing birds, as many birds are not sexually dichromatic and can only be reliably sexed visually during the breeding season, these findings could be the result of larger number of birds being listed as unknown sex than of unknown age. Seasonality also played a role in the prevalence of ticks parasitizing birds. Birds caught during the fall were more commonly parasitized by ticks than in any other season, likely coinciding with when larval rabbit ticks are in high abundance. Because very little is known about when different tick species are active during their various life stages, further studying investigating tick seasonality is mandated.

Because birds may be susceptible to various tick-borne pathogens and are unique in their abilities to travel thousands of kilometers in a relatively short period of time, they have the potential to spread disease pathogens much further and faster than other animals; therefore, an understanding of which avian species are parasitized by ticks is important to avian population dynamics and to human health. Although no new species were found during this study, other studies addressing bird-tick interactions have found non-native tick species on birds migrating through the area (Pietzsch 2008). Resident birds may also play an important role in the relationship among birds, ticks, and tick-borne disease pathogens as it is likely that resident birds serve as reservoirs for pathogens and therefore may affect the spread of pathogens both within and among species.

My study considered vegetation at the site level but not in enough detail within a site to test for within-site patterns that might predict tick parasitism. Future studies should conduct more extensive studies on the vegetation at each site. It is possible that tick abundance may be better predicted by vegetation characteristics at the finer site level than urbanization at the larger landscape scale. Because only gross categories of one vegetation type were made for each field site, analyses by vegetation type were not possible.

All studies have various limitations, and this study is no different. One limitation of this study was that I did not catch all species of birds present at the field sites, due to the biases of mistnetting. For example, I did not sample waterfowl, game species, or most high-flying avian species, as they were either too large to catch in mistnets or were species that do not regularly fly close to the ground, where my mistnets were set-up. Additionally, I did not conduct point counts at all of my field sites to determine which other species were present in comparison to what species were caught in mist nets. Another limitation was that I could not hold birds for long periods of time in order to allow any ticks parasitizing the birds to fall off when finished feeding, a method commonly used with mammals (Ostfeld 2000). Therefore, I likely did not find and collect all ticks found on all birds and probably misclassified some birds as being tick-free when they were not. Additionally, there were no unusual weather events such as hurricanes or blizzards that may have affected tick parasitism rates. Finally, because the majority of ticks collected in this study were rabbit ticks, many of the findings may not generalize to other tick species that parasitize birds.

As with any study, increasing the sample size of field sites would allow more power to tease apart predictive variables. There is a trade-off, however, between the frequency of sampling and the number of sites. Additional sites would allow confounds of urbanization to be addressed, though had I decreased sampling effort at permanent sites in order to increase efforts at ad-hoc sites, the power for permanent sites would have been reduced.

During this study, the majority of birds were not parasitized by ticks. Likely factors influencing parasitism rates include the various phenologies and behaviors of particular avian taxa; however, habitat also likely influences tick parasitism rates. For example, Carolina Wrens were commonly parasitized at rural sites but not at urban sites. Additionally, the probability of parasitism is also likely a function of individual behavior.

This research in particular was unique because I looked at the relationship among birds, ticks, and tick-borne diseases year-round, whereas similar studies have concentrated sampling during peak fall and spring migrations (Peters 2009). Previous studies likely focused on fall and spring migrations due to increased movement of birds during these times. Additionally, data collected by the many permanent banding stations around North America that are only open during fall and spring migrations are commonly addressed, further limiting analyses to areas that support permanent bird banding stations. This study demonstrated that ticks are found on birds year-round, though in variable proportions depending on the season, not solely during bird migration periods.

Overall, this study demonstrates the importance of understanding environmental factors, such as increasing urbanization, that affect the interactions between host and parasite. It also shows how complex the relationships among urbanization, birds, and ticks are and how many questions emerge from a seemingly simple study system.

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APPENDIX

APPENDIX: USGS GAP National Land Cover descriptions for southeastern coastal, Virginia (Homer et al. 2015).

Class	Name	Description
38	Evergreen Plantations or Managed Pine	Even-aged, regularly spaced forest stands established by planting and/or seeding in the process of afforestation or reforestation where individual trees are generally > 5 meters in height. Specifically, this class refers to plantations dominated by evergreen species.
103	Atlantic Coastal Plain Dry and Dry-Mesic Oak Forest	This system encompasses oak-dominated forests of somewhat fire-sheltered dry to dry-mesic sites in the coastal plain from southeastern Virginia to Georgia. It occurs in areas somewhat protected from most natural fires by some combination of steeper topography, isolation from the spread of fire, and limited flammability of the vegetation. If fires were more frequent, the vegetation would likely be replaced by more fire-tolerant southern pines, especially longleaf pine.
120	Atlantic Coastal Plain Mesic Hardwood and Mixed Forest	This upland system of the Atlantic Coastal Plain ranges from southern New Jersey south to Georgia in a variety of moist but non-wetland sites that are naturally sheltered from frequent fire. Such sites include lower slopes and bluffs along streams and rivers in dissected terrain, mesic flats between drier pine-dominated uplands and floodplains, and local raised areas within bottomland terraces or wet flats. Soils are variable in both texture and pH. The vegetation consists of forests dominated by trees that include a significant component of mesophytic deciduous hardwood species, such as beech or southern sugar maple. Upland and bottomland oaks at the mid-range of moisture tolerance are usually also present, particularly white oak, but sometimes also southern red oak, cherrybark oak, or Shumard oak. Loblolly pine is sometimes present, but it is unclear if it is a natural component or has entered only as a result of past cutting. Understories are usually well-developed. Shrub and herb layers may be sparse or moderately dense.
241	Atlantic Coastal Plain Nonriverine Swamp and Wet Hardwood Forest - Taxodium/Nyssa Modifier	This system consists of poorly drained, organic or mineral soil flats of the outer Atlantic Coastal Plain. These areas are saturated by rainfall and seasonal high water table without influence of river or tidal flooding. Fire is generally infrequent, but may be important for some associations. Vegetation consists of hardwood or mixed forests of *Taxodium distichum*, Nyssa spp., bottomland oaks, or other wetland trees of similar tolerance. The lower strata have affinities with pocosin or baygall systems rather than the river floodplain systems that have affinities with the canopy. The combination of canopy dominants and nonriverine, non-seepage hydrology distinguishes this system from other Coastal Plain systems. <u>Variation</u>: Taxodium/Nyssa - Deeper water expressions of this system dominated by bald cypress and/or water tupelo and swamp blackgum. <u>Other Variation(s)</u>: Oak.

APPENDIX Continued

242	Atlantic Coastal Plain Nonriverine Swamp and Wet Hardwood Forest – Oak Dominated Modifier	This system consists of poorly drained, organic or mineral soil flats of the outer Atlantic Coastal Plain. These areas are saturated by rainfall and seasonal high water table without influence of river or tidal flooding. Fire is generally infrequent, but may be important for some associations. Vegetation consists of hardwood or mixed forests of *Taxodium distichum*, *Nyssa* spp., bottomland oaks, or other wetland trees of similar tolerance. The lower strata have affinities with pocosin or baygall systems rather than the river floodplain systems that have affinities with the canopy. The combination of canopy dominants and nonriverine, non-seepage hydrology distinguishes this system from other Coastal Plain systems. <u>Variation</u>: Oak - Shallower water expressions of this system dominated by oaks (laurel, swamp white, swamp chestnut). <u>Other Variation(s)</u>: *Taxodium/Nyssa*.
246	Northern Atlantic Coastal Plain Basin Swamp and Wet Hardwood Forest	This system encompasses hardwood or mixed hardwood-conifer swamps of seasonally flooded non-riverine habitats in the Atlantic Coastal Plain from Long Island (New York), south to Virginia. The substrate is mineral soil, sometimes overlain by a layer of well-decomposed organic matter, but is not deep peat. The waters derive from overland flow collecting in the basin depressions, as well as some influence from groundwater seepage. Characteristic tree species include red maple, sweet gum, black gum, willow oak, and green ash. Loblolly pine is not uncommon south of Delaware Bay.
399	Atlantic Coastal Plain Peatland Pocosin	This system includes wetlands of organic soils on the outer terraces of the coastal plain from southeastern Virginia to the Carolinas. Occurring on broad flats or gentle basins, the vegetation is predominantly dense shrubland and very shrubby open woodlands. A characteristic suite of primarily evergreen shrubs, greenbriars, and pond pine dominates. These shrubs include inkberry, fetterbush, staggerbush, little leaf titi, big gallberry, and honeycups, along with laurel greenbrier. Pond pine is the characteristic tree, along with loblolly-bay, sweetbay, and swamp bay. Herbs are scarce and largely limited to small open patches. Under pre-European settlement fire regimes, stands of switch cane (canebrakes) would have been more common and extensive. Soil saturation, sheet flow, and peat depth create a distinct zonation, with the highest stature woody vegetation on the edges and lowest in the center. Catastrophic fires are important in this system, naturally occurring at moderate frequency. Fires generally kill all above-ground vegetation in large patches, which recovers rapidly in most of the burned areas, primarily by sprouting.

APPENDIX Continued

403	Atlantic Coastal Plain Northern Fresh and Oligohaline Tidal Marsh	These freshwater tidal marshes occur on the upper reaches of large rivers influenced by tidal flooding beyond the reach of saltwater. They are especially well developed on the Chesapeake and Delaware Bay drainages, and extend northeast to include portions of the Hudson River, Connecticut River, Merrimack River, Kennebec River and their tributaries, among others. The vegetation includes marshes dominated by tall grasses such as wild rice; marshes of lower stature dominated by forbs such as water hemp, rosemallow, and others; and vegetation characterized by ground-hugging rosette-forming herbs such as estuary pipewort and riverbank quillwort. Sediments of more protected spots are comprised finer-grained materials that are poorly drained, or of well-consolidated peat deposits. Areas with greater flooding force and scouring action have coarser mineral substrates such as sand and gravel.
450	Atlantic Coastal Plain Northern Tidal Salt Marsh	This system encompasses the intertidal marshes of the North Atlantic Coastal Plain from Chesapeake Bay north to Cape Cod, and sporadically to the mid-coastal Maine. It includes a number of different vegetation types including salt marshes, salt shrublands, and isolated salt "pannes" where only the most salt-tolerant species can grow. This system occurs on the bay (inner) side of barrier beaches and the outer mouth of tidal rivers where salinity is not much diluted by freshwater input. The typical salt marsh profile, from sea to land, features a low regularly flooded marsh strongly dominated by saltmarsh cordgrass; a higher irregularly flooded marsh dominated by saltmeadow cordgrass and saltgrass; low hypersaline pannes characterized by saltwort and other species; and a salt scrub ecotone characterized by marsh elder, groundsel-tree, and switchgrass. Salt marsh "islands" of slightly higher elevation also support eastern red-cedar. This system also includes the rare sea-level fens, which occur at the upper reaches of certain salt marshes where groundwater emerging from the uplands creates a distinctive freshwater peatland.
556	Cultivated Cropland	Areas used for the production of annual crops, such as corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards. Crop vegetation accounts for greater than 20 percent of total vegetation. This class also includes all land being actively tilled.
557	Pasture/Hay	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle. Pasture/hay vegetation accounts for greater than 20 percent of total vegetation.

APPENDIX Continued

567	Harvested Forest-Grass/Forb Regeneration	Areas dominated by herbaceous ground cover following tree harvesting.
568	Harvested Forest - Shrub Regeneration	Areas dominated by shrubs; less than 5 meters tall with shrub canopy typically greater than 20% of total vegetation. This class includes true shrubs, young trees in early successional stage or trees stunted from environmental conditions following a tree harvesting event.
575	Disturbed/ Successional – Shrub Regeneration	Areas where a relatively recent disturbance event has occurred, signs of which are still visible on the imagery (images acquired between 1999-2001) or identifiable using change detection techniques, and have regenerated to shrub or stunted tree dominated vegetation.
578	Open Water (Brackish/Salt)	All areas of open water, generally less than 25% cover of vegetation or soil. Specifically, coastal and near-shore estuarine and/or marine waters.
579	Open Water (Fresh)	All areas of open water, generally less than 25% cover of vegetation or soil. Specifically, inland waters of streams, rivers, ponds and lakes.
580	Quarries, Mines, Gravel Pits and Oil Wells	Areas of extractive mining activities with significant surface expression.
581	Developed, Open Space	Includes areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for less than 20 percent of total cover. These areas most commonly include large-lot single-family housing units, parks, golf courses, and vegetation planted in developed settings for recreation, erosion control, or aesthetic purposes.
582	Developed, Low Intensity	Includes areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20-49 percent of total cover. These areas most commonly include single-family housing units.
583	Developed, Medium Intensity	Includes areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50-79 percent of the total cover. These areas most commonly include single-family housing units.
584	Developed, High Intensity	Includes highly developed areas where people reside or work in high numbers. Examples include apartment complexes, row houses and commercial/industrial. Impervious surfaces account for 80 to100 percent of the total cover.

VITA

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EDUCATION
Old Dominion University, Norfolk, VA
Candidate, Masters of Science, Biology (Cumulative GPA: 4.00/4.00)
Advisor: Dr. Eric L. Walters
Expected Graduation: December 2015
Virginia Tech, Blacksburg, VA
Bachelor of Science, Wildlife Sciences (Cumulative GPA: 3.95/4.00)
Undergraduate Thesis: Habitat Management Plan: Golden-winged Warbler
Graduation: May 2011

SELECTED EXPERIENCE
Graduate Research Assistant – Bird/Tick Study (August 2012-August 2014)
Old Dominion University, Norfolk, VA; PI: Dr. Eric Walters
Graduate Teaching Assistant – General Biology (September 2015-August 2015)
Old Dominion University, Norfolk, VA; Director: Dr. Doug Mills

SELECTED AWARDS
National Science Foundation Graduate Research Fellowship Program (GRFP) (2014)
Selected as a recipient of a $132,000 grant that funds 3 years of graduate school
ODU Alumni Association Outstanding Scholar Fellowship ($1500)
Selected as a recipient of $1500 that helped fund my Master's research
Virginia Academy of Science (VAS) Small Research Grant (2013 & 2014)
Selected as a recipient of $1250 two years in a row to assist in funding field work

SELECTED PUBLICATIONS
(1) Heller, E. L., K. C. R. Kerr, N. F. Dahlan, C. J. Dove, and E. L. Walters. In Press. Overcoming challenges to morphological and molecular identification of Empidonax flycatchers: A case study from Virginia. Journal of Field Ornithology.
(2) Heller, E. L.*, C. L. Wright*, R. M. Nadolny*, W. L. Hynes, H. D. Gaff, and E. L. Walters. In Press. New records of *Ixodes affinis* (Acari: Ixodidae) parasitizing avian hosts in southeastern Virginia. Journal of Medical Entomology.
(3) Heller, E.L. J.A. Arnold, and E.L. Walters. 2015. Migrant bird research at Old Dominion University. Virginia Birds 11:4-5.